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JANUARY, 1940 RESEARCH BULLETIN 311

UNIVERSITY OF MISSOURI COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION

M. F. MILLER, *Director*

Studies on Fusarium Wilt of the Tomato

I. Immunity in *Lycopersicon pimpinellifolium Mill.* and Its Inheritance in Hybrids

G. W. BOHN AND C. M. TUCKER

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(Publication Authorized December 16, 1939)

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Studies on Fusarium Wilt of the Tomato

I. Immunity in *Lycopersicon pimpinellifolium Mill.* and Its Inheritance in Hybrids*

G. W. Bohn† and C. M. Tucker

1. INTRODUCTION

Fusarium wilt of the tomato is an old problem. It has been studied at some time during the past 30 years at most of the agricultural experiment stations in the southern half of the United States. It is most destructive in this region, occasionally killing entire fields of tomatoes before a crop has been harvested. Although losses caused by the disease have been reduced by the use of wilt-resistant tomato varieties and the practice of crop rotation, it still causes an annual loss of more than $1,000,000 to commercial tomato growers,[1] and in addition an uncalculated loss in home gardens.

2. THE DISEASE AND THE FUNGUS

A. The Disease

The first symptom of infection by *Fusarium lycopersici* Saccardo (1886) (*F. bulbigenum* var. *lycopersici* Wollenweber und Reinking (1935)) in a tomato plant in the field is yellowing of 1 or more of the lower leaves. The discoloration may be limited to 1 side of the leaf or the entire leaf may turn yellow, then wilt, shrivel, and become brown and dry. If such a leaf is removed from the plant, the extent of yellowing can be correlated with dark brown discoloration of 1 or both of the vascular traces.

As the fungus grows up the stem and enters other leaves, they, also, turn yellow, wilt, and die. The fungus frequently progresses most rapidly in a small group of vascular elements resulting in a characteristic distribution of leaf symptoms in but 1 branch or along 1 side of 1 branch. When the fungus reaches the upper part of the stem, the latter wilts from the tip back, the leaves and the upper part of the stem becoming brown and dry while the lower part

*In part from a thesis submitted by G. W. Bohn to the Graduate School of the University of Missouri in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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[1]Calculated from estimates of annual farm values of tomato crops in the United States reported by J. L. Orr et al. in the United States Department of Agriculture, Agricultural Statistics *1938*: 426-427 and estimates of tomato crop losses reported by J. I. Wood, Plant Disease Reporter Supplement *108*: 110-113 (1938).

of the stem may remain green and turgid and even produce new shoots. As the disease progresses, other parts of the plant are involved and the entire plant wilts and becomes brown and dry. Under environmental conditions very favorable to the progress of the disease, the leaves and stem tip may wilt, shrivel, and die without yellow discoloration. Under environmental conditions tending to inhibit the progress of the disease, the symptoms frequently are limited to yellowing of a few lower leaves; under such conditions the plant may become stunted or remain comparatively vigorous and produce fruits. Apparently healthy plants grown in Fusarium-infested soil frequently show brown discoloration of the vascular tissues; this is particularly true of commercial wilt-resistant varieties.

B. The Fungus

Fusarium lycopersici, the causal organism of the disease under discussion, is of the Elegans section of the genus Fusarium and is closely related to several other vascular parasites of crop plants. The fungus is a facultative parasite which grows in soil and various liquid and solid culture media. Different isolates of the fungus differ in cultural characteristics, physiology, and virulence. Isolates may produce abundant cottony tufts of aerial mycelium or an effuse growth restricted to the surface of the culture medium. Young hyphae are hyaline, but blue and red insoluble pigments frequently are produced in older hyphae, especially on acid media. Unicellular, ellipsoidal, hyaline microconidia and 3- to 5-septate, falcate, hyaline macroconidia are produced in scattered sporodochia. Intercalary and terminal chlamydospores with thick, brown walls are produced occasionally in old cultures.

The fungus invades the host through uninjured root tissues and enters the xylem. It grows in the xylem elements up the root and stem and into the leaves. The invaded tissues may be traced by dark brown discoloration.

3. THE PREVALENCE OF *FUSARIUM LYCOPERSICI*

Fusarium wilt of the tomato has been reported from all of the 48 states excepting Maine, Vermont, South Dakota, and Wyoming.[2] Outside of the United States, the disease has been reported in Mexico, Jamaica, Puerto Rico, British Guiana, Suriname, Argentina, Chile, British Columbia, England and Wales, Russia, Latvia, Germany, Austria, Italy, Bulgaria, Egypt, Rhodesia, South Africa, Mauritius,

[2]Data obtained from the United States Department of Agriculture, Bureau of Plant Industry, Plant Disease Reporter and Supplements, and a personal letter from Dr. H. A. Edson, Division of Mycology and Disease Survey; reports and other publications of agricultural experiment stations in the United States and other countries; and in personal letters from plant pathologists and agriculturalists in the United States and elsewhere.

India, West China, Victoria, Western Australia, Queensland, New South Wales, Fiji, New Zealand, and Hawaii.

The disease is most destructive in warm climates and is serious only in greenhouses in its northern range. Devastating losses have been reported in various tomato growing regions of the United States. Orton (1902a, 1903) reported that Fusarium wilt caused great injury to tomatoes in Florida in 1902 and a loss of $500,000 in that state in 1903, besides causing large areas of land to be abandoned "as the disease prevents the planting of tomatoes more than 1 year on the same land.". Serious losses have been reported in Arizona and Louisiana by Orton (1906, 1907), in Florida by Rolfs (1907), in Virginia by Fromme and Thomas (1916), in greenhouses in Indiana by Gardner (1919a), in Maryland by Jones (1922), in Illinois by Tehon (1923) and Yount (1923), in California by Shapovalov and Lesley (1924), in Delaware by Adams (1923), in Arkansas by Elliot (1924), in several states east of the Mississippi River and south of the Ohio River by Weber and Ramsey (1926), in Mississippi by Wedgeworth, Neal, and Wallace (1927) and in Colorado by LeClerge (1930).

Although it is possible that some losses attributed to *Fusarium lycopersici* were caused by other agents as indicated by Bryan (1924) and Shapovalov (1924), it is apparent that the disease is destructive in many parts of the United States.

4. METHODS OF COMBATTING *FUSARIUM LYCOPERSICI*

A. Prevention of Infection

Since *Fusarium lycopersici* enters the tomato plant through the roots and progresses through vascular tissues, the futility of attempts to control the disease with sprays applied to the stems and leaves was pointed out by Massee (1895) and many others. According to Elliot and Crawford, (1922), Pritchard (1922), Edgerton and Moreland (1920), and others, *F. lycopersici* is introduced into new soils on seeds and in plants grown in infested soil in seedbeds. The latter applies particularly to southern-grown seedlings transplanted in northern states as indicated by Bullock (1937). Because *F. lycopersici* grows well as a saprophyte in a wide range of culture media, including soil, it is probable that it grows indefinitely in soils into which it has been introduced, as suggested by Edgerton and Moreland (1920), Higgins (1925), and Altstatt and Young (1936).

The nature of the parasite and its method of attack limit control measures to (1) the use of seeds, treated or untreated, free from the parasite; (2) sterilization of seedbed soils with steam (Noble et al., 1937) or chemicals (Young, 1939); (3) clean cultivation, including

the removal of diseased plants and prevention of the introduction of the parasite into new soils on cultivating equipment, shoes, and fertilizers; (4) rotation of crops to reduce the abundance of *Fusarium lycopersici;* and (5) the use of wilt-resistant varieties. Although the disease can be controlled in seedbeds and green houses by steam or by soil fungicides, these methods are expensive and frequently unsatisfactory as stated by Wenholz (1935), Zimerly (1919), Huelsen and Gillis (1930), and others. Durst (1917, 1918), Edgerton and Moreland (1920), and Birmingham (1921) concluded that soil fungicides were of no practical value for controlling the disease in the field.

B. The Development of Resistant Varieties of Tomatoes

Following the researches of Orton (1902b, 1908, Webber and Orton, 1901) on the development of varieties of melon, cowpea, and cotton resistant to Fusarium wilt diseases, and Bolley's (1903) studies on the resistance of flax to Fusarium wilt, attempts to obtain varieties of tomatoes resistant to *Fusarium lycopersici* were started by investigators at various agricultural experiment stations in the United States, and more recently in other parts of the world.

In the United States, tests for resistance to Fusarium wilt in the tomato were started in Florida in 1905 by Rolfs (1907, 1913), in Tennessee in 1910 by Essary (1912), in Louisiana in 1909 by Edgerton and Moreland (1913), in Maryland in 1912 by Norton (1912, 1914), in Illinois in 1913 by Durst (1917, 1918), in Ohio in 1915 by Green and Humbert (1918), at the Arlington Experiment Farm in 1915 by Pritchard (1922), in Georgia in 1916 by Higgins (1917) and Stuckey (1917), in Indiana in 1919 by Gardner (1919b, 1920), in Missouri in 1919 by Quinn (1922), in Kansas in 1919 by Melchers and Scott (White, 1926), in California in 1923 by Shapovalov and Lesley (1924, Lesley and Shapovalov, 1925), in Michigan in 1934 by Strong (1939). The tests initiated in Illinois by Durst were continued in 1925 by Huelsen and Gillis (1926, 1930), later by Huelsen and Michaels (1933) and Huelsen (1934, 1936, 1939). Tests in Florida were renewed in 1932 by Weber and Kelbert (1932, 1937). Essary's program in Tennessee was continued by Sherbakoff and Andes (1935, 1937). The investigations begun at the Arlington Experiment Farm were continued by Porte (1932, 1936), Wellman, and others (Boswell, 1937). Investigations were started in Missouri in 1934 by Tucker and Bohn (1936, 1937) and in Ohio by Alexander (1937).

On other continents, tomatoes were tested for resistance to *Fusarium lycopersici* in the Eastern Transvaal, South Africa by Wager (1930, 1934) and in Australia by Shirlow (Wenholz 1932, 1935, 1936, 1937, 1939) and Pollock (1925).

Some improvements in methods of testing tomatoes for resistance to Fusarium wilt have been made. Early tests of resistance, such as those of Essary (1912) and Norton (1914) were conducted in fields naturally infested with *Fusarium lycopersici*. Edgerton (1915) and Moreland (Edgerton and Moreland 1920, 1921), Green and Humbert (1918), Pritchard (1922), and others practiced artificial infestation of greenhouse and field soils to reduce the numbers of plants escaping infection. Edgerton (1915) reported the use of sterilized soils containing large proportions of organic matter and the maintenance of relatively high temperatures (27 to 29 degrees C.) to test the resistance of tomato plants in the seedling stage. This permitted the elimination of susceptible plants in the greenhouse and increased the opportunities to study the effects of various environmental factors and different isolates of *F. lycopersici* on the development of the disease. Artificial infestation of greenhouse and field soils culminated in the work of Strong (1939), who infested test soils with 50 isolates of *F. lycopersici* from 14 of the 48 states and from Australia, and South Africa. Wellman (1939) immersed the roots of seedlings in a suspension of hyphae and spores; the seedlings were then planted in soil held at temperatures favorable for the development of wilt.

In addition to improvements in methods of conducting resistance tests, improvements have been made in breeding methods. Essary (1912, 1914), Durst (1917, 1918), Pritchard (1922), and others noticed differences in reaction to Fusarium wilt within varieties as well as between varieties. Pritchard (1922) divided tomato varieties into 3 classes on the basis of their reactions: (1) susceptible varieties yielding only susceptible progenies from selected individuals with apparent resistance; (2) resistant varieties yielding progenies with the same degree of resistance from all individuals; and (3) varieties yielding resistant and susceptible progenies from different individuals. Although some mass selections were made (Essary, 1912), many of the first wilt-resistant varieties were produced by single plant selection within the third class of varieties described by Pritchard. Essary (1914) selected Tennessee Beauty from Beauty, Norton (1917) and Pritchard (1922) selected Norton from Stone.

Because most of the wilt-resistant varieties and selections were inferior to the favored commercial varieties in other important characters, crosses were made between resistant selections and susceptible varieties. Edgerton and Moreland (1920, 1921) developed Louisiana Red and Louisiana Pink from a cross between Louisiana-Wilt-Resistant, selected from Acme, and Langdon's Earliana, an early, prolific, susceptible variety. Pritchard (1927) developed the variety Marglobe from a cross between Marvel, a resistant selection from Merveille des

Marchés, and Globe, a variety with slight resistance but better fruit characters. Break O'Day (Pritchard, 1932) was produced from a cross between Marglobe and Marvana, a resistant selection from a cross between Marglobe and Earliana (an early, susceptible variety). White (1926) with Melchers and Scott, developed Kanora from a cross between Norton, resistant, and John Baer, susceptible, as a wilt-resistant variety adapted to Kansas conditions. Huelsen and Gillis (1930) crossed Louisiana Pink with Grand Rapids Forcing to obtain Lloyd Forcing and Blair Forcing, wilt-resistant varieties for greenhouse culture.

The Fusarium wilt-resistant varieties of tomatoes now on the market have proved valuable in many regions of the United States, as indicated by the comments of growers and research workers (Edson and Wood, 1937; Goodwin, 1928; Manns, 1937; Shapovalov, 1924; Wedgeworth et al. 1927; Wellington, 1920). Some of these varieties have been introduced in Italy (Pastore, 1935), South Africa (Wager, 1933), and Australia (Wenholz, 1932; Noble et al., 1937) where they have been found valuable in reducing losses from Fusarium wilt.

These varieties are not immune to *Fusarium lycopersici*. Edgerton and Moreland (1920) suggested that the "wilt-resistant" varieties should be called "tolerant" rather than "resistant" because they wilt and die under conditions very favorable for the development of Fusarium wilt. Serious losses in plantings of wilt-resistant varieties of tomatoes have been reported in various regions of the United States by McClintock (1920a, 1924), Valleau (1923), Bach (1928), Taubenhaus (1930), Essary (1933, 1934), Allen and Talbert (1934), Miller (1936), and Cook (1935). Reports by growers and home gardeners of losses from wilt and the continued interest of gardeners, growers, and research workers in the problem indicate that the resistant varieties, although much better than susceptible varieties, do not always exhibit satisfactory resistance. During the past few years, increasing attention has been devoted to attempts to obtain a variety of tomato more resistant to Fusarium wilt.

Several workers have attempted to obtain varieties with greater degrees of resistance by crossing different resistant varieties and selections. Pritchard (1926) crossed Norton, resistant, with Duke of York, resistant, to obtain Norduke, which he considered more resistant than either parent. Higgins (1927, 1931, 1937) crossed different resistant selections and varieties in attempts to combine factors for resistance. He reported the F_1 hybrids were more susceptible than either parent. Similar methods have been used by Weber and Kelbert (1932 to 1937, inclusive), Sherbakoff and Andes (1935, 1936, 1937), and others. Shapovalov and Lesley (1937) and Lesley and Shapova-

lov, (1937) crossed Cal. 2, selected for resistance to Verticillium wilt, with Marvana, a Fusarium-resistant variety developed by Pritchard (1932), to obtain the variety Riverside, resistant to both diseases.

The search for tomatoes resistant to Fusarium wilt was limited to varieties of *Lycopersicon esculentum* by most workers until 1932. However, in 1916, Pritchard (1922) found 1 collection of the Currant Tomato, *L. pimpinellifolium* Mill. as susceptible as commercial varieties of *L. esculentum.* In Australia, Shirlow (Wenholz 1932, 1935, 1936, 1937, 1939) used a collection of *L. pimpinellifolium* in breeding experiments to develop varieties of tomatoes resistant to *F. lycopersici, Cladosporium fulvum* Cooke, bronze wilt, and spotted wilt. He found Fusarium-resistance associated with small fruit size, but reported, "one line of the Earliana-Red Currant-Earliana cross in the third generation is homozygous for resistance to Fusarium wilt, and carries a heavy crop of fruit of good size (Wenholz, 1936). Young (1939) reported 2 lines from crosses involving Red Currant received from Shirlow through Wenholz were not more resistant than various commercial varieties in Texas.

Tucker and Bohn (1936, 1937) tested accessions of *Lycopersicon esculentum, L. pimpinellifolium,* and species in other genera of the Solanaceae in 1934. All accessions of *L. esculentum* were susceptible in some degree. Accessions of Solanum and Physalis were immune. Accessions of *L. pimpinellifolium* varied in reaction; some were very susceptible, 1 was resistant, and 1 was apparently immune to *Fusarium lycopersici.* First generation hybrids between the immune accession and Bonny Best proved immune in greenhouse tests in the fall of 1935, indicating that immunity was dependent on dominant genetic factors. These workers (1939) stated that data on later generations, to be reported in detail here, demonstrated that the expression of immunity to *F. lycopersici* in *L. pimpinellifolium* Accession 160 was governed in inheritance by a single, dominant genetic factor.

In 1937, Alexander (1937) reported an attempt to "synthesize a higher type of resistance" by crossing highly resistant selections of Louisiana Pink, Marvel, and *Lycopersicon pimpinellifolium.* He also reported the initiation of tests of a large collection of domestic tomatoes and "wild relatives" in an attempt to find a higher type of resistance.

Boswell (1937) reported that Porte and Wellman found one line of *Lycopersicon pimpinellifolium* to be practically immune to *Fusarium lycopersici* and highly resistant to a number of leaf diseases in 1935. In personal correspondence, it has been determined that the immune line used by Porte and Wellman is identical with Bohn and Tucker's Accession 160, received from Porte in 1934. Wellman and

Blaisdell (1939) reported that Red Currant tomatoes (*L. pimpinellifolium*) were resistant to 30 isolates of *F. lycopersici* but were slightly more infected by raised than by appressed forms. Wellman (1939) reported that *L. pimpinellifolium* "has retained perfect resistance in the field under severe conditions that result in killing of all adjacent, fully susceptible plants." Some plants, the roots of which had been immersed in a water suspension of *F. lycopersici,* were stunted when grown in soil in the greenhouse under controlled conditions. "There was no obvious yellowing or wilting of leaves," and the plants recovered, "developing flowers and fruits as successfully as noninoculated disease-free plants."

5. THE PROBLEM

Preliminary experiments indicated that available tomato varieties did not possess factors of sufficient potency to protect them from wilt when exposed to a virulent isolate under favorable conditions for wilt development (Table 1).

A search for a more resistant species, variety, or strain for use as breeding material was started early in 1934. Botanists in various parts of the world were requested to send collections of species of Solanum and Lycopersicon, particularly uncultivated forms collected in South America, the continent on which this group of plants originated. The large number of responses to these requests indicated the general interest of plant pathologists and other botanists in the problem.

Table 1.—Resistance to *Fusarium lycopersici* in tomato varieties grown in infested soil in the greenhouse and inoculated at transplanting. Columbia, Missouri. 1934.

Tomato Variety	Number Set	Percentages Alive	"Healthy"*	Uninfected†
Marglobe	790	17.2	2.2	0.0
Pritchard	885	22.9	1.6	0.0
Break O'Day	770	20.3	1.8	0.1
Norton	800	27.0	3.9	0.0
Louisiana Pink	710	30.1	1.5	0.0
Globe	225	12.2	1.2	0.0
Stone	203	12.3	0.5	0.0
Earliana	206	5.3	0.0	0.0
Bonny Best‡	864	6.3	0.5	0.0

*Plants which developed no external symptoms of Fusarium wilt were recorded as "Healthy".
†Plants without brown-discolored vascular tissues typical of Fusarium infection were recorded as "Uninfected".
‡The Bonny Best plants were grown in steamed, non-infested soil in the greenhouse. Plants of other varieties were grown in infested soil in the greenhouse.

Tests of resistance were made as the material became available but it was not possible to test all accessions. The discovery, early in the tests, of an accession of *Lycopersicon pimpinellifolium* with apparent immunity to the disease led to a breeding program to develop a tomato variety with immunity or a high degree of resistance.

6. METHODS USED IN TESTS OF RESISTANCE TO *FUSARIUM LYCOPERSICI*

A. Test Methods

Resistance to *Fusarium lycopersici* in accessions, selections, and hybrids was tested at Columbia, Missouri during the period 1934 to 1939. Most of the tests were conducted as combined greenhouse and field tests, but some plants were tested only in the greenhouse and others, only in the field. Efforts were made to maintain optimum conditions in the greenhouse for wilt development.

1. Greenhouse.—The experiments of Edgerton (1915), Edgerton and Moreland (1920), Clayton (1923a), and White (1927) demonstrated that Fusarium wilt of tomatoes develops most rapidly at temperatures of 27 to 29 degrees C. with occasional periods when the temperature rises to 30 or 31 degrees. The experiments of Clayton (1923b) on moisture; those on soil reaction by Edgerton and Moreland (1920), Sherwood (1923), Scott (1924), White (1927), and Pritham and Anderson (1937); and on nutrition by Clayton (1923b), Ahmet (1933), Fisher (1935), and Cook (1937) indicated that extreme conditions may affect the development of the disease, but that, in general, environmental conditions favorable for the growth of the tomato plant are also favorable for the development of Fusarium wilt. The ability of *Fusarium lycopersici* to cause wilt in the tomato is not seriously affected by moisture, soil reaction or plant nutrients within the ranges usually regarded as optimum for the crop. Steam sterilized soils and soils high in organic content were reported by Edgerton (1918) to increase wilt through increases in amounts of *F. lycopersici* in such soils.

Soil mixtures for greenhouse tests were made by screening and mixing thoroughly 2 parts garden loam, 2 parts leaf mold or spent mushroom compost, and 1 part sand. In 1934, 1935, and 1936 the soil mixtures were steamed at 18 to 20 pounds pressure for 2 hours; thereafter, the mixtures were steamed in a concrete bin for 6 hours, with steam entering the soil at 3 to 6 pounds pressure. Pots and flats were steamed with the soil or dipped in an aqueous solution of formaldehyde (1/50) or boiling water.

The steamed soils were infested with pure cultures of *Fusarium lycopersici* grown in flasks of sterilized cornmeal or oats. In most of the tests each pot or flat was infested with a single isolate. Several isolates were used in 1934 and 1935. From 1936 to 1938, with the exception of the test of isolates (Text pages 31-34), 1 virulent isolate, F 7[3], was used to infest all greenhouse soils.

[3]Appendix: list of Fusarium isolates.

In 1939 cultures of F 7 and F 5b were mixed at infestation. In 1934 and 1935, equivalent weights of the fungus and culture medium (cornmeal) were mixed with the soil in test pots. Thereafter, equivalent volumes, sufficient to wet all seeds and the entire soil surface, of strained spore and mycelium suspensions in water were added to the test pots before the seeds were covered. Check plantings were made in steamed, non-infested soil.

Seeds were planted in replications varying from 14 to 100. Seeds of commercial varieties were planted in replications of 25 to 60. Seeds of accessions were planted in replications of 25 or 50 in pots and in replications of 50 or 100 in flat rows, depending on the available supply of seeds. Hybrid progenies from crosses involving *Lycopersicon pimpinellifolium* Accession 160 were planted in replications of 14 to 50; replications of progenies from hand-pollinated flowers were limited to 35 seeds.

The pots and flats were placed on greenhouse benches and the environmental conditions were maintained so far as possible to favor development of Fusarium wilt. The temperatures of soil and air varied considerably in all experiments, but generally were maintained between the minimum and maximum limits (20 and 33° C.) for the development of Fusarium wilt in tomatoes, as determined by Clayton (1923a). During the first years fairly wide fluctuations occurred, but in 1938 and 1939 excellent temperature control with a high degree of uniformity was obtained.

Wilted plants were removed from the soil, cut and examined for brown discoloration of the vascular tissues, and counted at intervals of 1 to 10 days. Frequent examinations of young seedlings were necessitated by rapid drying out of the small plants after wilting. Older plants were killed less rapidly and the time intervals between examinations were increased.

Final greenhouse data were taken when the plants were set in the field. Plants too small to set in the field or broken in handling were dissected and examined for vascular discoloration. All plants with external or internal symptoms of wilt visible by reflected or transmitted light and the runts and broken plants with brown-discolored vascular tissues were included in the greenhouse data as infected plants.

2. Field.—Plants with no symptoms of Fusarium infection were transplanted directly from the original pots or flats to the field. The practice of growing the plants in a crowded, warm environment in the greenhouse caused them to be more spindling and tender than was desirable for field setting. They were placed outdoors for a few days before transplanting, and set deep in the field (about 10 inches).

The plot of ground used for the field tests is located on the South Farms of the University of Missouri. The soil is Putnam silt loam, of medium fertility and with a tight clay subsoil. This type of soil does not absorb or retain moisture well and is especially poor in drought seasons; it is generally considered unsuitable for truck crops. The plot had been used for a corn crop in 1933 and had not been cropped with tomatoes before this series of experiments was started. It was used for the tests from 1934 to 1939, inclusive, with one small application of barnyard manure.

Six half-liter oat cultures of *Fusarium lycopersici* were mixed with each 40 gallons of water used in transplanting operations; the partially covered root system of each plant was watered with 1 pint of the suspension of the fungus and oats. Bonny Best checks grown in autoclaved, non-infested soil in the greenhouse, but inoculated at transplanting, were set in cross rows between groups of 5 test plants in the first 4 years, between groups of 10 test plants in 1938, and in rows replicated frequently in 1939.

Most of the plants killed by agents other than *Fusarium lycopersici* were lost early in the seasons. In 1935 and 1938 many were washed out by torrential rains. In all years, some were broken by the wind and killed by cut worms. Plants lost immediately after setting were replaced in 1934 and 1935. It was necessary to keep complete records from emergence to the ends of the seasons on all plants in hybrid progenies; therefore, no resetting was done in later years. During 1939 very few plants were lost from factors other than Fusarium infection.

Individual plant records were taken at intervals of 3 to 4 weeks in the years 1935 to 1938; weekly examinations were made in 1939. External symptoms of wilt were verified by examination of leaf traces. At the ends of the seasons, all living plants were dug and examined for brown vascular discoloration.

The data reported are limited to presence and absence of infection without regard to severity of symptoms. All plants with definite symptoms of Fusarium infection, however slight, were recorded as infected. Most of the plants were exposed in the greenhouse to infection by virulent isolates of *F. lycopersici* in steamed, artificially infested soil, high in organic content; and, in addition, were inoculated as they were set in the field. A few plants of susceptible and resistant commercial varieties of *Lycopersicon esculentum* apparently escaped infection but these were rare.

B. Analytical Methods

Analyses of variance of emergence data on 7 commercial varieties of tomatoes[4] in 1934 and on line progenies of 4 commercial resistant varieties[5] in 1935 demonstrated that *Fusarium lycopersici* had no effect on emergence of tomato seedlings (Table 2). Accordingly, all calculations on resistance were based on the numbers of seedlings.

Table 2.—Analysis of variance of data on emergence of tomato seedlings from seeds planted in autoclaved soil, non-infested and infested with 4 virulent isolates of *Fusarium lycopersici*. Columbia, Missouri. April, 1935.

Variation caused by differences in means of	D.F.	Sums of Squares	Variances	F Values		
				Obtained	Probability 0.05	0.01
Varieties	3	668.566667	222.855556	5.99	2.76	4.13
Treatments ..	5	370.266667	74.053333	1.99	2.37	3.34
Replications ..	4	309.950000	77.487500	2.08	2.52	3.65
Var. x Treat. .	15	295.133333	19.675555	...	2.07	2.87
Var. x Repl. .	12	2609.516666	217.459722	5.85	1.92	2.50
Treat. x Repl.	20	661.650000	33.082500	...	1.84	2.42
Error	60	2231.283333	37.188056	...	...	...

Some plants in accessions and progenies were too small to set in the field; others were broken in handling, failed to become established, or were killed by agents other than *Fusarium lycopersici*. Percentages of infection in the field were obtained by dividing the numbers of plants wilted and infected by the net field samples after the discarded and lost plants were deleted. To obtain approximations of the percentages of susceptible plants in segregating populations from crosses between Accession 160 and commercial varieties of tomatoes, it was necessary to estimate the proportions of suscepts[6] among the discarded and lost plants. It was assumed that the discarded and lost plants included the same proportions of suscepts as the net field samples. The calculated numbers of suscepts among the discarded and lost plants were added to the actual numbers that wilted or were infected in the greenhouse and field. The resulting total numbers were divided by the numbers of seedlings to obtain the final percentages of suscepts. Percentages of infected plants in accessions were calculated the same way.

There were several sources of error which probably caused the calculated percentages of suscepts to differ from the percentages obtainable had every plant been grown to maturity and classified. Plants too small to set in the field or damaged by handling were examined for vascular discoloration and infected plants were included in the greenhouse data. Non-infected plants were recorded as "discarded."

[4]Four resistant varieties, Marglobe, Break O'Day, Pritchard, and Norton; the "intermediate" variety Globe; and 2 susceptible varieties, Stone and Earliana.
[5]Marglobe, Break O'Day, Norton, and Louisiana Pink.
[6]The term "suscepts" indicates non-immune plants; differences in the degree of susceptibility were not considered.

The assumption that these discarded, non-infected plants contained as many suscepts as the net field sample is probably erroneous since the "discarded" lots were subjected to more rigorous examination than the field samples. The latter, of course, were not cut for examination as were the "discarded" lots. Hence, the calculated percentages of suscepts tend to be greater than the true percentages.

Some plants were broken by the wind, killed by insects, or failed to survive transplanting. It is probable that infected plants were more susceptible to injuries from these causes. The necessary assumption that such plants were susceptible in the same proportions as those of the net field samples tended to cause the calculated percentages of suscepts to be smaller than the true percentages. However, this source of error was not involved in data on plants grown in non-infested soil in the greenhouse. Transplanting losses occurred very soon after transplanting, and Fusarium infection initiated after setting could hardly have been a factor.

Hybrids with growth habits similar to that of Accession 160 were more slender than those bearing more resemblance to the commercial parents; these slender plants were more susceptible to wind and cultivation injuries. Although linkage of genes for immunity and plant structure was not studied, the latter is apparently complex in heredity and it is possible that plants most similar to Accession 160 were more likely to have genes for immunity. If this is true, the plants lost from mechanical injuries included a disproportionately large percentage of immune plants, resulting in an increase of the calculated over the true percentages of suscepts.

In addition to errors due to discarded and lost plants there were some errors in classification. A few plants of susceptible and resistant varieties escaped infection. It seems certain that some susceptible plants in segregating populations also escaped infection and were classified with the immune phenotype. This was proven by progeny tests of some plants. Occasional plants of Accession 160, its line progenies, and F_1 hybrids of this accession with susceptible varieties had small discolored strands of vascular tissues resembling, somewhat, the more conspicuously browned tissues caused by *Fusarium lycopersici* in commercial varieties. Plants with these small, discolored strands were occasionally classified as susceptible, especially in 1936. Progeny tests of such plants in segregating populations indicated that they were genetically immune. Accordingly, they were recorded separately in 1937, 1938, and 1939, and included in the immune phenotype in the data presented. When there was any doubt concerning the proper classification of a plant with discolored vascular tissues, it was included in the susceptible phenotype.

Because of these sources of error, the calculated percentages of suscepts in the segregating populations cannot be considered as accurate as percentages of phenotypes in populations segregating easily visible characters that do not affect survival (e. g. red vs. yellow color of the fruit flesh). However, as the various sources of error tend to balance one another, the calculated percentages are considered to be fairly correct approximations.

7. RESISTANCE TO *FUSARIUM LYCOPERISCI* IN VARIOUS ACCESSIONS OF THE SOLANACEAE

A. Tests of Accessions in Genera Other Than *Lycopersicon*

In greenhouse tests in which Bonny Best was used as a check on experimental methods all accessions of Solanum, Physalis, Nicandra, Lycium, and Capsicum were free from infection.[7]

The results, in agreement with those of Sherbakoff (1918), Harter and Weimer (1920) and McClintock (1920a, 1920b, 1924), indicate that the parasitism of *Fusarium lycopersici* is limited to the genus Lycopersicon.

B. Tests of Accessions of *Lycopersicon esculentum*

Various varieties and un-named collections of *Lycopersicon esculentum* were tested for resistance to *Fusarium lycopersici.* (Appendix, A, list of accessions tested). Some of these were tested in steamed, infested soil in the greenhouse; some were inoculated and set in the field; and a few were tested in both greenhouse and field. The accessions were compared with Bonny Best (susceptible), Break O'Day (resistant) and Louisiana Pink (resistant). Tests made at different times often yielded different results; therefore, only plantings made simultaneously were regarded as comparable.

Most of the accessions of *Lycopersicon esculentum* were apparently as susceptible to *Fusarium lycopersici* as the check commercial varieties. A few plants among several accessions remained free from vascular discoloration throughout the growing seasons of 1936-1938. The numbers that apparently escaped infection varied in proportion with the opportunity for infection provided by the various treatments. Although there was considerable variation in the severity of wilt symptoms in different accessions, all accessions of *L. esculentum,* with one exception (Fusarium-wilt-resistant John Baer), grown in infested soil in the greenhouse and inoculated at transplanting were more than 90 percent infected. Few plants escaped infection even if they were exposed only to the residual Fusarium present in the soil from previous crops.

[7]See Appendix, List of Accessions.

The behavior of certain accessions developed as wilt-resistant strains or varieties, and a few others, was of particular interest. The previously mentioned exception, Fusarium-wilt-resistant John Baer,[8] selected by Strong (1939), was tested in the field in 1937. Observations on the severity of external symptoms and degree of vascular discoloration, as well as the exceptionally high percentage of disease-free plants (27.9), indicated that this selection may be more resistant than Break O'Day and Louisiana Pink. Progenies from open-pollinated flowers of 10 plants that were free from infection or had slight vascular discoloration were tested in the green house and field in 1938. The percentages of suscepts in these progenies (95.7) indicated that this selection was quite susceptible to Fusarium infection.

Myco 1, Accession 102, received from Fahmy (1932) as a selection practically immune to Fusarium wilt and highly resistant to root knot nematodes in Egypt, was tested in the field in 1936. This variety had about the same degree of resistance as Break O'Day and Louisiana Pink.

Observations on a few plants of Cherry tomato, Accession 157, tested in 1935, indicated that this strain was very resistant to Fusarium wilt. Only 1 of 11 seedlings grown in infested soil developed symptoms of wilt in the greenhouse. Bonny Best and Break O'Day wilted 90.7 and 61.1 percent, respectively, under identical treatment and conditions. Although the remaining 10 plants became infected in the field, 8 of these did not develop external symptoms of the disease and there was only slight discoloration of the vascular tissues at the end of the season. Bonny Best, Break O'Day, and Louisiana Pink, treated like Accession 157, showed external symptoms in 96.2, 50.3, and 61.9 percent respectively.

C. Tests of Accessions of *Lycopersicon pimpinellifolium*

Accessions of the Red Currant tomato, *Lycopersicon pimpinellifolium*, were tested for resistance from 1934 to 1939. Susceptible accessions of *L. esculentum* grown under comparable conditions served as checks.

Of the 10 accessions tested, 9 exhibited degrees of susceptibility that rendered them undesirable as breeding stocks (Table 3).

Accession 160[9] was apparently unaffected by the 5 isolates of *Fusarium lycopersici*[10] used to infest steamed soil in different flats in which the seeds were planted. (Table 3). There was no wilting or yellowing

[8]This is a sib of the selection described by Strong in the publication cited and is considered by her to be inferior to the latter.

[9]Accession 160 was received from Dr. W. S. Porte, U. S. Dept. of Agri., Washington, D. C., who wrote of it, ". . . our No. 2116 was obtained by F. P. I. from Dr. Wolcott, who picked it up near Trujillo, Peru." Dr. George N. Wolcott stated in correspondence that the collection was made in late 1928 or early 1929.

[10]F 6, F 7, F 11, F 12, and F 13. (Appendix, list of Fusarium isolates.)

Table 3.—Resistance to *Fusarium lycopersici* in accessions of *Lycopersicon pimpinellifolium* in the greenhouse and field. Columbia, Missouri. 1934-1939.

Variety	Accession	Treatment*	Greenhouse		Field		Total
			Seedlings	Infected	Sample	Infected	Infected Percent†
Red Currant	10	A	480	265	...	...	55.2
Red Currant	16	A	38	31	...	...	81.6
Red Currant	17	A	43	30	...	...	69.8
Red Currant	25	A	324	129	...	...	39.8
Red Currant	145	A	49	22	...	...	44.9
Red Currant	146	A	48	22	...	...	45.8
Red Currant	159	A	479	205	45	45	100.0
Red Currant	160	A	430	0	209	0	0.0
Red Currant	174	A	149	32	45	45	100.0
Red Currant	491	A	95	82	13	13	100.0
Red Currant	279	B	...	...	40	38	95.0
Red Currant	490	A	...	...	17	7	41.2
Yellow Currant	281	B	...	...	39	27	69.2

*A. Grown in infested soil in the greenhouse and inoculated at transplanting.
B. Grown in non-infested soil in the greenhouse and inoculated at transplanting.
†The method of calculating total percentages of infected plants is described on Text page 16.

of the leaves and no indications of vascular discoloration could be seen by transmitted light. Plants in infested soil could not be distinguished from the checks. Under identical conditions 61.1 percent of Break O'Day plants wilted and some accessions of *Lycopersicon esculentum* wilted to the extent of 99 percent.

At the conclusion of the greenhouse test, plants of Accession 160 were inoculated as they were set in the field. The plants were set in 5 replications of 45 plants each. Plants not set in the field were cut and examined for brown discoloration of the vascular tissues of the stems and roots. None of these plants had discolored tissues.

Resistant and susceptible accessions of *Lycopersicon esculentum* and *L. pimpinellifolium* served as checks in the field. Although some of the checks, particularly *L. esculentum* Accession 157 and *L. pimpinellifolium* Accession 159, had considerable resistance, as indicated by the severity of symptoms, every plant became infected.

A few plants of Accession 160 either were killed by insects or were washed out. The remaining plants grew vigorously and fruited abundantly. The plants were thin-stemmed, spreading and procumbent; they filled the spaces left by Bonny Best check plants (in transverse rows) which wilted early in the season. Figure 1 shows the condition of a section of the test plot on September 18, 1935 when row 20 contained 1 apparently healthy and 3 wilted Bonny Best plants; row 21 had 5 apparently healthy and 21 wilted Norton plants; row 22 contained 43 healthy plants of Accession 160; row 23 had 13 apparently healthy and 21 wilted plants of Illinois Pride; and row 24, a single wilted plant of Accession 195 ("wild" *L. esculentum* from Dr. Wakabayashi, Hawaii).

Twenty plants of Accession 160 were removed and examined on August 25; all were free from brown vascular discoloration and ap-

Fig. 1.—Section of the tomato wilt test plot, South University Farms, Columbia, Missouri, September 18, 1935. Explanation in the text.

peared entirely normal. The remaining plants were examined in the laboratory at the end of the growing season. Although all plants of other accessions of Lycopersicon had brown discolored vascular tissues typical of Fusarium wilt, either above or below the soil line, none of the plants of Accession 160 showed symptoms of infection. Longitudinal and cross sections of typical stems of Accession 160 and commercial varieties of *L. esculentum* are shown in Figures 2 and 3. The brown discoloration of vascular tissues adjacent to the pith, characteristic of stems infected with *Fusarium lycopersici* and clearly visible in the stems of Bonny Best (Figure 2, left) and Break O'Day (Figure 2, right and Figure 3, below), were absent from stems of Accession 160 (Figures 2, center and 3, above). There were some very small, filiform, dark brown streaks, 5 to 20 millimeters long, in the woody tissues of a few plants. These streaks did not resemble those resulting from Fusarium infection. Isolations on plain and acidified potato-dextrose-agar did not yield growth of any type. Isolations from infected stems of accessions of *L. esculentum* yielded *F. lycopersici* without exception.

The ability of *Fusarium lycopersici* to infect Accession 160 under extreme conditions was tested in heavily infested soil in the greenhouse from June 18 to July 27, 1935. Two virulent isolates, F 6 and F 11, were grown on autoclaved barley seeds. A layer, 1 inch thick, of the

Fig. 2.—Longitudinal sections of typical stems of Bonny Best (left), Accession 160 (center), and Break O'Day (right), grown in the tomato wilt test plot, South University Farms, Columbia, Missouri. 1935.

seeds overgrown by the isolates was placed in each pot of autoclaved soil and covered with 1 inch of soil. Twenty seeds of Accession 160 were planted in one half of each pot; in the other halves were planted 20 seeds of Bonny Best, Norton, and Break O'Day. The experiment was run in triplicate; sterile barley seeds were placed in the checks. Since the roots of all seedlings penetrated the barley cultures, all test plants were equally exposed to the fungus.

Fig. 3.—Cross-sections of typical stems of Accession 160 (above) and Break O'Day (below) grown in the tomato soil test plot, South University Farms, Columbia, Missouri. 1935.

The plants of the commercial varieties, without exception, developed symptoms of wilt within 39 days. None of the plants of Accession 160 showed external symptoms or evidence of infection in the stems.

Plants of Accession 160 and the varieties of *Lycopersicon esculentum* in the check pots remained free from Fusarium infection.

8. IMMUNITY TO *FUSARIUM LYCOPERSICI* IN LINE PROGENIES OF *LYCOPERSICON PIMPINELLIFOLIUM* ACCESSION 160

A. Tests of Plants Grown in the Greenhouse and Field

Line progenies of *Lycopersicon pimpinellifolium* Accession 160 were tested from 1936 to 1939. "Accession 160" is used in all further discussions to designate this accession and its line progenies. A few of the progenies tested were obtained from self-pollinated flowers. Since F_1 hybrids between Accession 160 and commercial varieties were easily recognized by their larger fruits and various plant characters, the few chance hybrids were eliminated from progenies from open-pollinated flowers and the data on both types of line progenies were combined. Although a few plants of check accessions had no vascular discoloration, the high percentages of wilt and infection in these varieties indicated that the methods, Fusarium isolates, and environmental conditions were favorable for infection each year, (Table 4).

Table 4.—Summary of data on reactions of Accession 160 and commercial varieties of tomatoes to Fusarium wilt in the greenhouse and field, Columbia, Missouri. 1936 to 1939.

Reaction Type	Year	Treatment*	Greenhouse		Field	Added	Total
			Seedlings	Infected	Infected Number	Suscepts† Number	Suscepts‡ Percent
Accession 160							
Immune	1936	A	284	0	0	0	0.0
Immune	1936	B	75	0	0	0	0.0
Immune	1937	A	485	4?	5?	4?	2.3?
Immune	1937	B	31	0	0	0	0.0
Immune	1938	A	392	2?	4?	1?	1.8?
Immune	1938	B	24	0	0	0	0.0
Immune	1939	A	347	0	0	0	0.0
Commercial Varieties							
Resistant	1936	A	1080	496	424	1337	96.1
Resistant	1936	B	155	0	246	237	89.5
Resistant	1937	A	328	26	193	103	98.2
Resistant	1937	B	199	0	122	208	91.7
Resistant	1938	A	691	461	130	93	99.0
Resistant	1938	B	85	0	570	293	93.6
Resistant	1939	A	552	357	78	117	100.0
Resistant	1939	B	215	0	215	0	100.0
Commercial Varieties							
Susceptible	1936	A	872	490	77	305	100.0
Susceptible	1936	B	208	6	223	1121	98.2
Susceptible	1937	A	423	156	116	151	100.0
Susceptible	1937	B	180	0	665	707	95.5
Susceptible	1938	A	567	528	...	...	91.4
Susceptible	1938	B	129	0	1436	596	99.8
Susceptible	1939	A	812	642	131	39	100.0
Susceptible	1939	B	857	0	857	0	100.0

*Treatment A, seeds planted in steamed, infested soil and inoculated at transplanting.
Treatment B, seeds planted in steamed, non-infested soil and inoculated at transplanting.
†Added suscepts were calculated suscepts among those lost and discarded.
‡Total percentages were calculated on the numbers of seedlings plus additional plants set in the field.

Of 1882 plants of line progenies of Accession 160 tested in the greenhouse and 1674 plants tested in the field, all remained healthy and free from external symptoms of wilt. Ten plants had very small, dark brown strands of tissue adjacent to the pith and continuous for considerable distances in the stems (Table 4). These strands were much less conspicuous than those in infected commercial varieties. The health and vigor of these 10 plants suggested that the small brown strands were not caused primarily by *Fusarium lycopersici*. Other observations on discoloration in plants grown in the field or greenhouse suggested that this type of discoloration occurred in non-infected plants.

In a greenhouse test in 1939 in which soil and moisture conditions were unfavorable for growth of tomato plants, 10 of 81 plants of Accession 160 had small brown strands of vascular tissues. Four of the 10 plants with discolored tissues were grown in non-infested soil. Unidentified Fusaria were isolated from 2 plants; and an unidentified fungus with green spores was isolated from a third plant. In a greenhouse test of F_1 hybrids between Accession 160 and Bonny Best, several plants were attacked by *Phytophthora parasitica* Dast. and the roots were rotted; two of these plants had discolored vascular tissues which yielded cultures of *F. lycopersici*. Similar strands of discolored tissues were observed in 2 field-grown pepper plants (*Capsicum annuum L.*). Potato-dextrose-agar isolations from 1 pepper plant yielded Penicillium, Aspergillus, and various bacteria; the tissues of the other were apparently sterile.

Three other types of discoloration occurred in the stems of plants grown in the field in the years 1936 to 1939: (1) Small, filiform, discontinuous, brown to black strands were observed in the vascular tissues of the lower parts of the stems and the tap roots. Isolations from such tissues occasionally yielded various fungi and bacteria but usually proved sterile. A few of these strands were traced to small, dead roots. It seems probable that the discoloration was caused by substances absorbed from the dead roots. These strands were noticed, also, in a few plants of the original accession tested in 1935. (2) Diffuse, general, light brown discoloration occurred in the vascular tissues and frequently involved the entire tap root and lower part of the stem. This type of discoloration was mistaken for Fusarium injury the first day plants were classified in 1936. Repeated attempts to isolate micro-organisms from such tissues were not successful. The tissues were apparently sterile, and the discoloration was attributed to environmental factors, particularly changes in moisture content of the soil. Vascular discoloration in tomato stems was attributed to excessive irrigation by Blood (1936). Cook (1937) re-

ported discoloration of apparently sterile stem tissues of tomatoes. (3) Dark brown discoloration of the vascular tissues and pith was caused by breaks in the stems between large branches near the soil line. These wounds were caused by wind, cultivation, and rough handling of the plants while combatting blister beetles. This type of discoloration was similar to that caused by *F. lycopersici*. However, it could be distinguished by tracing the discolored strands to their points of origin; furthermore, the strands originating at wounds did not extend long distances in the stems.

In 1939, all plants that showed any type of discoloration were cultured on potato-dextrose-agar. Two hundred seventy bits of tissue from 90 plants failed to yield Fusarium. Discoloration was associated with poor drainage conditions.

It is possible that some plants of Accession 160 were classified as doubtfully infected as the result of confusion of wilt symptoms with 1 or more of the other types of discoloration occurring in the stems. It is probable that *Fusarium lycopersici* can invade plants injured by other parasites, unfavorable environmental conditions, insects, or other agents. Young (1939) reported a decrease of the wilt-resistance of commercial varieties of tomatoes attacked by *Heterodera marioni* (Cornu) Goodey.

Of more than 2535 plants of Accession 160 and its line progenies tested in these experiments, only 20 showed discoloration of the type indicative of possible infection by *Fusarium lycopersici*. None of the plants developed any external symptoms of Fusarium wilt, and it is probable that other factors, environmental or parasitic, contributed to the occasional discoloration observed. It is apparent that *Lycopersicon pimpinellifolium* Accession 160 exhibited near-immunity to *F. lycopersici* in these experiments. There was no yellowing, wilting, dwarfing, or other external symptoms indicative of Fusarium infection. The fact that *F. lycopersici* does invade occasional plants indicates that immunity is not absolute; however, the absence of external symptoms and the failure of the fungus to affect adversely the growth of the plants indicate a practical immunity. The term "immunity" will be used to distinguish this exceptionally high degree of resistance from the type known in the commercial resistant varieties; the latter is not effective under environmental conditions favorable for the development of the disease.

B. Tests of Plants Injected With Suspensions of *Fusarium lycopersici*

The immunity of Accession 160 was tested in the greenhouse in 1936 by injecting a suspension of the spores and mycelium of *Fusa-*

rium lycopersici Isolate F 7 directly into the stems, just above the soil line, with a Luer medical syringe and needle. The suspension was made by shaking 10 milliliters of sterile tap water with a young potato-dextrose-agar culture. It contained approximately 20 microspores and a few macrospores and bits of mycelium within the limits of the high power field of the compound microscope. The stems of Accession 160 were very slender and only 0.2 and 0.1 milliliters of the suspension were injected. Bonny Best plants were injected with 0.5, 0.2 and 0.1 milliliters of the suspension. Sterile tap water was injected into the stems of check plants. The injections caused a temporary translucent appearance of the stems, but the wounds healed well with the exception of 1 plant of Accession 160 injected with water. The stem of this plant was split and swollen in the region of the puncture, probably due to excessive mechanical injury. Eventually the plant produced callus tissue and remained healthy (Table 5).

Table 5.—Reactions of plants injected with suspensions of *Fusarium lycopersici*. Greenhouse. Columbia, Missouri. 1936.

Accession, Variety, or Cross	Injection February 8	Condition of Host Plant		
		February 23	March 8	May 1
Accession 160	0.2 ml. water	Healthy	Healthy	Healthy
Accession 160	0.2 ml. water	Healthy, but split and swollen	Healthy	Healthy
Accession 160	0.2 ml. F 7	Healthy	Healthy	Healthy
Accession 160	0.1 ml. F 7	Healthy	Healthy	Healthy
Bonny Best	0.5 ml. water	Healthy	Healthy	Healthy
Bonny Best	0.5 ml. water	Healthy	Healthy	Healthy
Bonny Best	0.5 ml. F 7	Lower leaves yellow	Dead	.....
Bonny Best	0.5 ml. F 7	Lower leaves yellow	Wilted	Dead
Bonny Best	0.2 ml. F 7	Lower leaves yellow	Dead	.....
Bonny Best	0.2 ml. F 7	Wilted	Dead	.....
Bonny Best	0.1 ml. F 7	Lower leaves yellow	Wilted	Dead
Bonny Best	0.1 ml. F 7	Healthy	Healthy	Dead
F_1 Hybrid	0.2 ml. water	Healthy	Healthy	Healthy
F_1 Hybrid	0.2 ml. water	Healthy	Healthy	Healthy
F_1 Hybrid	0.2 ml. F 7	Healthy	Healthy	Healthy
F_1 Hybrid	0.2 ml. F 7	Healthy	Healthy	Healthy
F_1 Hybrid	0.2 ml. F 7	Healthy, but split and swollen	Healthy	Healthy
F_1 Hybrid	0.1 ml. F 7	Healthy	Healthy	Healthy

Some of the Bonny Best plants had symptoms of Fusarium wilt 10 days after inoculation; all but 1 developed symptoms within 15 days and were dead or nearly dead after 28 days (Figure 4, left). The Bonny Best plant which appeared healthy after 28 days developed symptoms of wilt a few days later; it persisted for some time and produced new shoots after the main stem died; the whole plant was dead after 51 days (May 1). Bonny Best plants injected with sterile tap water remained healthy (Figure 4, right).

Fig. 4.—Bonny Best plants twenty-five days after injection with water (right) and Fusarium Isolate F 7 (left).

None of the plants of Accession 160 developed symptoms of the disease at any time (Table 5 and Figure 5). They were used for breeding work after the experiment was completed.

These tests demonstrated that the immunity of Accession 160 to *Fusarium lycopersici* is not dependent upon mechanical resistance to invasion and suggest that its immunity is attributable to physiological factors. The results also demonstrate that the immunity of Accession 160 to *F. lycopersici* is not limited to the cortex of the root as suggested for wilt-resistance in various host plants by Brown (1936).

Fig. 5.—Plants of *Lycopersicon pimpinellifolium* Accession 160 twenty-five days after injection with water (left) and Fusarium Isolate F 7 (right).

C. Tests of Plants Grown in Soil Infested With Various Isolates of *Fusarium lycopersici*

Little is known of the occurrence of physiologic forms of *Fusarium lycopersici.* Edgerton and Moreland (1920) found several isolates to differ in virulence. However, each isolate exhibited the same relative virulence to all varieties of tomatoes tested. They concluded that these results, and the observation that a resistant variety selected in a climate very favorable for the disease is also resistant in other regions, "tend to disprove the suggestion that there may be different strains of the wilt fungus in different parts of the country." Shapovalov and Lesley (1924) found one isolate pathogenic and another, saprophytic. They expressed the opinion that differences in percentages of infection in different varieties were due to differences in varieties rather than differences in Fusarium strains. White (1927) found isolates to differ in virulence and in growth in various culture media. He established two groups based on virulence and cultural characteristics; he did not test their relative virulence to different varieties of tomatoes. Haymaker (1928) reported that the relative virulence of single isolates from each group established by White was constant with different varieties of tomatoes and under different conditions. He concluded, "breeding tomatoes resistant to Fusarium wilt is not so complicated as breeding cereals resistant to rust," and, "there would be no value in attempts to establish varieties or forms of *Fusarium lycopersici.*" Wellman and Blaisdell (1939) correlated virulence of 30 isolates to Bonny Best (susceptible), Marglobe (resistant), and Red Currant (highly resistant) with cultural characteristics. They did not mention differential pathogenicity of isolates to the varieties.

Yarnell et al. (1930) observed that Fusarium wilt of tomatoes occurs in a number of soil types in Texas, indicating that the fungus is adapted to a variety of soil reactions or that several strains of the fungus occur in Texas. McWhorter and Parker (1929) stated, "the resistance of a variety varies in different localities, a phenomenon attributed largely to strain variations of the causal organism." These statements were not supported by experimental evidence.

Experiments in 1934 and 1935 on virulence of different isolates[11] of *Fusarium lycopersici* from diseased tomato plants in Missouri and Kansas, indicated that different isolates of the fungus differ considerably in virulence. Isolates more virulent to Bonny Best were also more virulent to Marglobe. In analyses of variance based on survival means, the variation caused by the interaction between varieties and

[11]Isolates F 6, F 7, F 11, F 12, and F 13. (Appendix B).

Fusarium isolates was equal to the variation attributed to experimental error; there was no indication of differential pathogenicity of the isolates toward different varieties. Isolates very virulent to 1 variety were also virulently pathogenic to the others. Isolate F 7 was more virulent than the others, and was used to infest the soil in greenhouse and field tests in 1936, 1937, and 1938; and, with Isolate F 5b, in 1939.

Although differential pathogenicity of isolates of *Fusarium lycopersici* has not been reported in the literature and was not indicated in the experiments of 1934 and 1935, it was considered advisable to test the immunity of *Lycopersicon pimpinellifolium* Accession 160 with a collection of isolates of *F. lycopersici* from various geographic areas and tomato varieties. Forty-three isolates,[12] received from investigators in various parts of the world and obtained from infected tomato plants that occurred in the experiments were used to infest steamed soil in which seeds of Accession 160 (immune), Break O'Day (resistant), and Bonny Best (susceptible) were planted in July, 1937.

During the first 6 weeks the environmental conditions were not favorable for the development of Fusarium wilt and several plants in some pots were killed by damping-off fungi and insects; therefore, the data are not reported in detail. Isolate F 7 caused the largest percentages of infection in uncontaminated pots of Break O'Day and Bonny Best, 84.7 and 88.3 percent, respectively. None of the plants of Accession 160 developed any symptoms of Fusarium infection either during growth or when the plants were cut for examination at the termination of the experiment.

Some of the isolates were apparently non-pathogenic to tomatoes. The data on these were substantiated and they were eliminated when the stocks were recovered from Earliana plants grown in steamed, infested soil.

The immunity of Accession 160 to 33 recovered isolates and 6 others was tested in the greenhouse in 1938. The data on the check varieties, Bonny Best and Marglobe, indicated that the methods and environmental conditions were favorable for infection and wilting (Table 6). Some of the isolates, F 1, F 3, F 5b, F 20, F 31, and F 34, killed all seedlings of these varieties within 40 to 48 days after planting. Although there was considerable variation in the numbers of plants killed and infected and in the time required for killing, all of the isolates were pathogenic to Bonny Best and Marglobe. There was little indication of differential pathogenicity to the 2 check varieties; all isolates, with the possible exceptions of F 36 and F 51, were more virulent toward Bonny Best than toward Marglobe.

[12]Appendix, B: List of Fusarium isolates.

Table 6.—Immunity to various isolates of *Fusarium lycopersici* in *Lycopersicon pimpinellifolium* Accession 160. Greenhouse. Columbia, Missouri. 1938.

Fusarium Isolate	Tomato Variety	Number of Seedlings	Percentages		
			Wilted	Infected	Healthy
F 1	Bonny Best	101	100.0	0.0	0.0
F 1	Marglobe	54	100.0	0.0	0.0
F 1	Acc. 160	95	0.0	0.0	100.0
F 2	Bonny Best	95	55.8	35.8	8.4
F 2	Marglobe	72	1.4	40.3	58.3
F 2	Acc. 160	96	0.0	0.0	100.0
F 3	Bonny Best	93	100.0	0.0	0.0
F 3	Marglobe	59	100.0	0.0	0.0
F 3	Acc. 160	87	0.0	0.0	100.0
F 5a	Bonny Best	85	96.7	3.5	0.0
F 5a	Marglobe	55	69.1	21.8	9.1
F 5a	Acc. 160	93	0.0	0.0	100.0
F 5b	Bonny Best	91	100.0	0.0	0.0
F 5b	Marglobe	59	100.0	0.0	0.0
F 5b	Acc. 160	97	0.0	0.0	100.0
F 6	Bonny Best	84	91.7	8.3	0.0
F 6	Marglobe	57	64.9	31.6	3.5
F 6	Acc. 160	98	0.0	0.0	100.0
F 7	Bonny Best	88	100.0	0.0	0.0
F 7	Marglobe	46	67.4	28.5	4.3
F 7	Acc. 160	105	0.0	0.0	100.0
F 10	Bonny Best	95	27.4	2.1	70.5
F 10	Marglobe	72	15.3	15.3	69.4
F 10	Acc. 160	109	0.0	0.0	100.0
F 13	Bonny Best	83	100.0	0.0	0.0
F 13	Marglobe	63	57.1	28.6	14.3
F 13	Acc. 160	93	0.0	0.0	100.0
F 14	Bonny Best	91	100.0	0.0	0.0
F 14	Marglobe	61	65.6	31.1	3.3
F 14	Acc. 160	98	0.0	0.0	100.0
F 15	Bonny Best	84	100.0	0.0	0.0
F 15	Marglobe	48	100.0	0.0	0.0
F 15	Acc. 160	94	0.0	0.0	100.0
F 16	Bonny Best	83	100.0	0.0	0.0
F 16	Marglobe	45	84.4	11.1	4.5
F 16	Acc. 160	99	0.0	0.0	100.0
F 17	Bonny Best	77	85.7	?	?
F 17	Marglobe	39	56.4	35.9	7.7
F 17	Acc. 160	92	0.0	0.0	100.0
F 20	Bonny Best	93	100.0	0.0	0.0
F 20	Marglobe	52	100.0	0.0	0.0
F 20	Acc. 160	94	0.0	0.0	100.0
F 22	Bonny Best	81	100.0	0.0	0.0
F 22	Marglobe	46	73.9	21.7	4.4
F 22	Acc. 160	105	0.0	0.0	100.0
F 23	Bonny Best	75	100.0	0.0	0.0
F 23	Marglobe	46	84.8	15.2	0.0
F 23	Acc. 160	96	0.0	0.0	100.0
F 24	Bonny Best	85	78.8	15.3	5.9
F 24	Marglobe	53	58.5	26.4	15.1
F 24	Acc. 160	96	0.0	0.0	100.0
F 25	Bonny Best	73	100.0	0.0	0.0
F 25	Marglobe	35	94.3	5.7	0.0
F 25	Acc. 160	85	0.0	0.0	100.0
F 26	Bonny Best	85	62.4	14.1	23.5
F 26	Marglobe	51	27.5	43.1	29.4
F 26	Acc. 160	99	0.0	0.0	100.0

Fusarium Isolate	Tomato Variety	Number of Seedlings	Percentages		
			Wilted	Infected	Healthy
F 28	Bonny Best	93	88.2	10.7	1.1
F 28	Marglobe	64	60.9	23.5	15.6
F 28	Acc. 160	81	0.0	0.0	100.0
F 29	Bonny Best	81	100.0	0.0	0.0
F 29	Marglobe	50	84.0	4.0	12.0
F 29	Acc. 160	73	0.0	0.0	100.0
F 30	Bonny Best	88	100.0	0.0	0.0
F 30	Marglobe	58	86.2	5.2	8.6
F 30	Acc. 160	92	0.0	0.0	100.0
F 31	Bonny Best	30	100.0	0.0	0.0
F 31	Marglobe	45	100.0	0.0	0.0
F 31	Acc. 160	85	0.0	0.0	100.0
F 32	Bonny Best	83	77.1	10.8	12.1
F 32	Marglobe	53	49.1	22.6	28.3
F 32	Acc. 160	87	0.0	0.0	100.0
F 33	Bonny Best	70	100.0	0.0	0.0
F 33	Marglobe	58	87.9	12.1	0.0
F 33	Acc. 160	94	0.0	0.0	100.0
F 34	Bonny Best	80	100.0	0.0	0.0
F 34	Marglobe	44	100.0	0.0	0.0
F 34	Acc. 160	96	0.0	0.0	100.0
F 36	Bonny Best	77	96.1	2.6	1.3
F 36	Marglobe	49	100.0	0.0	0.0
F 36	Acc. 160	96	0.0	0.0	100.0
F 37	Bonny Best	78	84.6	0.0	15.4
F 37	Marglobe	52	67.3	23.1	9.6
F 37	Acc. 160	100	0.0	0.0	100.0
F 40	Bonny Best	63	92.1	7.9	0.0
F 40	Marglobe	58	67.2	19.0	13.8
F 40	Acc. 160	105	0.0	0.0	100.0
F 41	Bonny Best	85	95.3	4.7	0.0
F 41	Marglobe	57	96.5	0.0	3.5
F 41	Acc. 160	91	0.0	0.0	100.0
F 43	Bonny Best	72	54.2	23.6	22.2
F 43	Marglobe	65	32.3	26.2	41.5
F 43	Acc. 160	98	0.0	0.0	100.0
F 44	Bonny Best	67	91.0	6.0	3.0
F 44	Marglobe	57	82.5	17.5	0.0
F 44	Acc. 160	92	0.0	0.0	100.0
F 45	Bonny Best	86	83.7	14.0	2.3
F 45	Marglobe	58	67.2	19.0	13.8
F 45	Acc. 160	98	0.0	0.0	100.0
F 46	Bonny Best	82	92.7	0.0	7.3
F 46	Marglobe	49	81.6	8.2	10.2
F 46	Acc. 160	100	0.0	0.0	100.0
F 47	Bonny Best	85	81.2	12.9	5.9
F 47	Marglobe	57	43.8	21.1	35.1
F 47	Acc. 160	100	0.0	0.0	100.0
F 48	Bonny Best	88	100.0	0.0	0.0
F 48	Marglobe	56	78.6	16.1	5.3
F 48	Acc. 160	96	0.0	0.0	100.0
F 49	Bonny Best	77	68.8	6.5	24.7
F 49	Marglobe	57	52.6	10.5	36.9
F 49	Acc. 160	95	0.0	0.0	100.0
F 50	Bonny Best	80	90.0	3.8	6.2
F 50	Marglobe	54	70.4	18.5	11.1
F 50	Acc. 160	88	0.0	0.0	100.0
F 51	Bonny Best	93	87.1	9.7	3.2
F 51	Marglobe	46	89.1	10.9	0.0
F 51	Acc. 160	96	0.0	0.0	100.0

None of the 39 isolates was pathogenic to Accession 160. All plants of this accession were healthy and free from internal discoloration when the final data were taken. The results support the opinion that plants of Accession 160 do not develop wilt caused by *Fusarium lycopersici*. In addition, they demonstrate that the immunity of this accession is not restricted to isolates from a few locations but extends to isolates from various parts of North America and other continents.

9. IMMUNITY TO *FUSARIUM LYCOPERSICI* IN HYBRIDS OF *LYCOPERSICON PIMPINELLIFOLIUM* ACCESSION 160 WITH VARIETIES OF *L. ESCULENTUM*

A. Cross-pollinations Between Immune and Susceptible Plants

Lycopersicon pimpinellifolium has been crossed with *L. esculentum* by numerous investigators. Sturtevant (1889) stated, "the various so-called species of the tomato cross with facility," and suggested that the number of species should be reduced to 2. Although there may be some question that Sturtevant included crosses between *L. esculentum* and *L. pimpinellifolium*, hybrids between these species were reported by Bailey (1891), Munson (1892), Rane and Hunt (1897), and many others. *L. pimpinellifolium* has been used in crosses with *L. esculentum* to develop commercial varieties of tomatoes resistant to *Cladosporium fulvum* by Sengbusch and Loschakowa-Hasenbush (1932), Osmun (1934), Alexander (1934, 1938), Guba (1934, 1936, 1939), and Langford (1937). Alexander (1938) found a lethal linked with the single factor for immunity or extreme resistance; Langford (1937) placed the factor for immunity in the fourth linkage group and found additional factors for resistance in the third and fifth linkage groups. Crosses between the 2 species were made in attempts to develop a tomato variety with better flavor by Sengbusch and Weissflog (1933); to develop varieties resistant to *Fusarium lycopersici* and other fungi, as well as virus diseases, by Shirlow (Wenholz, 1932, 1935 to 1938); and to develop varieties resistant to *F. lycopersici* by Tucker and Bohn (1936, 1937, 1939), Wellman and others (Boswell, 1937), and Alexander (1937). Yeager (1937) crossed *L. esculentum* with *L. pimpinellifolium* in attempts to develop varieties with extreme earliness. MacArthur (1926) and Lindstrom (1935) found nearly all known genetic factors of *L. pimpinellifolium* dominant over those of *L. esculentum*. Powers (1939a, 1939b) studied the effects of different regions of chromosome I on quantitative characters (number of locules and size of fruits) in hybrids between these species. The cytology of hybrids between the 2 species was studied by Afify (1933), Lindstrom and Humphrey

Fig. 6.—An F_1 hybrid between *Lycopersicon pimpinellifolium* Accession 160 and the Earliana variety of *L. esculentum*. Fruits set from hand-pollinated flowers. Columbia, Missouri. March 4, 1936.

(1933) and Humphrey (1937). All found hybrids between *L. pimpinellifolium* and *L. esculentum* easily obtainable and highly fertile; Humphrey (1937) expressed the opinion that geneticists probably would prefer to consider them varieties of 1 species.

During the summer of 1935, seeds were obtained from crosses of *Lycopersicon pimpinellifolium* Accession 160 with Earliana and Bonny Best. The F_1 hybrids were somewhat intermediate between the parent species in appearance, but resembled *L. pimpinellifolium* more than the commercial varieties. They set fruits readily to self-pollinations and to pollinations made with pollen of the parent species, (Figure 6). Examination of pollen from potted plants grown in the greenhouse, February 26, 1936 yielded the following listed percentages of viable pollen: Bonny Best, 47 percent (1182 grains); Accession 160, 50 percent (641 grains); F_1 hybrid, 54 percent (165 grains). Although the percentages were low, probably because of adverse environmental conditions, especially light, the figures indicate that the hybrid produces viable pollen in as large proportions as does either parent. Examination of pollen-mother-cells of F_1 hybrids indicated that meiosis was normal. Crosses between Accession 160 and various accessions of *L. esculentum,* including stocks with various genetic marker genes were made in 1936 and 1937. All F_1 hybrids were apparently alike in spite of marked differences in the *L. esculentum* parents; and all were quite fertile, setting fruits readily to controlled and natural pollinations.

In addition to crosses with Accession 160, Bonny Best (susceptible) was crossed with *Lycopersicon pimpinellifolium* Accession 159 (resistant) and *L. esculentum* Accession 157 (resistant Cherry). These were 2 small-fruited accessions that were infected by *Fusarium lycopersici,* but apparently possessed more resistance than commercial varieties, as indicated by external symptoms and growth of the plants in the field in 1935.

B. Immunity in F_1 Progenies

F_1 progenies from crosses between Bonny Best and Accessions 157, 159 and 160 were tested for resistance to Fusarium Isolates F 3 and F 11 during the winter of 1935-1936. Fusarium wilt was apparent in the Bonny Best plants and in the F_1 hybrids of this variety with Accessions 157 and 159 when the plants were 20 days old. None of the plants of Accession 160 or its F_1 hybrids with Bonny Best showed external symptoms of wilt. Two F_1 hybrids affected by root rot caused by *Phytophthora parasitica* also yielded cultures of *F. lycopersici.*

Mice dug into the soil for wheat seeds used in the inoculum and caused losses, directly and indirectly, in nearly all pots. Therefore, the experiment was discarded. Some of the F_1 hybrids of Accession 160 with Bonny Best served as breeding material.

Some F_1 hybrids of Accession 160 with Bonny Best were included in the stem inoculation experiment discussed above (Text pages 26-

Fig. 7.—F_1 hybrids of Accession 160 with Bonny Best 25 days after injection with water (left) and Fusarium Isolate F 7 (right).

28). Two plants injected with water, 3 plants injected with 0.2 milliliter of a suspension of Fusarium Isolate F 7, and 1 injected with 0.1 milliliter of the suspension remained healthy throughout the experiment and were used as pistillate parents. (Figure 7 and Table 5.).

Additional F_1 progenies from crosses of Accession 160 with various susceptible accessions were tested in combined greenhouse and field experiments in 1936 and 1937. Although other types of discoloration occurred in the vascular tissues of some of these plants, most of them were free from possible symptoms of Fusarium infection when the plants were removed at the ends of the seasons (Table 7). A few plants had small, brown strands in the vascular tissues, similar to those occurring in line progenies of Accession 160. These plants were large and vigorous, and had no external symptoms of wilt; they differed from the other F_1 plants only in the occurrence of the discolored strands. Although all of the plants with discolored strands occurred in progenies which had commercial varieties as pistillate parents, these plants did not result from accidental self-pollinations; such plants would have been recognized in non-segregating populations by their habit of growth, hairy stems, and large fruits.

The occurrence of occasional plants with these small, discolored strands in Accession 160 may indicate immunity is not absolute. Their more frequent occurrence in F_1 hybrids of this accession with susceptible varieties may indicate the factor, or factors, governing the heredity of this character is, or are, not completely dominant over the factor, or factors, for susceptibility. It is possible, however, that these strands were caused by other agents or resulted from invasions by Fusarium in a secondary role. (Text pages 25, 26, 36).

Table 7.—Immunity to *Fusarium lycopersici* in F_1 hybrids of Accession 160 with susceptible accessions in the greenhouse and field. Columbia, Missouri. 1936, 1937.

Accessions Crossed*	Year Tested	Treatment†	Greenhouse		Field		Calc. Added Susc.	Total Suscepts Percent
			Seedlings	Infected	Sample Net	Infected Number		
14 x 160	1936	B	...	...	9	0	0	0.0
183 x 160	1936	B	...	...	15	0	0	0.0
180 x 160	1936	B	...	...	4	0	0	0.0
160 x 366	1937	A	47	0	34	0	0	0.0
366 x 160	1937	A	122	0	79	2?	1?	2.5?
5 x 160	1937	A	100	4?	60	2?	1?	7.0?
487 x 160	1937	A	190	4?	132	11?	4?	10.0?
490 x 160	1937	A	19	0	...	...	...	0.0
183 x 160	1937	A	47	0	...	...	...	0.0

*Pistillate parents precede staminate parents in statements of crosses. Accessions 160 (immune) and 490 (susceptible) were collections of *Lycopersicon pimpinellifolium*. Other accessions were *L. esculentum*. (Appendix, A).

†Treatment: A, plants grown in infested soil in the greenhouse and inoculated at transplanting; B, plants grown in non-infested soil in the greenhouse and inoculated at transplanting.

C. Immunity in Progenies From Back-crosses to Accession 160

Progenies from first back-crosses of Earliana x Accession 160 to Accession 160 were tested in the greenhouse and field in 1936. None of the plants wilted during the season or had typical symptoms of Fusarium infection when the plants were examined at the end of the season (Table 8). Small, brown strands of tissue similar to those in Accession 160 and the F_1 hybrids occurred in the stems of 4 plants. Fusarium was isolated from the discolored tissues of 3 of these plants.

Fusarium Isolate F 40, from 1 of the back-cross plants, was apparently non-pathogenic to Accession 160, Bonny Best, Break O'Day, and Earliana. Isolates F 44 and F 45 from back-cross plants, and Isolates F 34, F 36, and F 37, from F_1 hybrids, were pathogenic to Earliana. These 5 isolates were non-pathogenic to Accession 160 in the second test of Isolates (Table 6). Isolates F 34 and F 36 were virulently pathogenic toward Bonny Best and Marglobe; Isolates F 37, F 44, and F 45 were apparently less virulent. Several isolates from commercial varieties were as virulent toward Bonny Best and Marglobe as were those from hybrids. There was no evidence that the isolates from F_1 and BC_1 hybrids were pathogenic to Accession 160 or more virulently pathogenic to commercial varieties than other isolates. The discolored strands in these plants did not result from infection by exceptionally virulent strains. The occurrence of a non-parasitic isolate among those obtained from small, brown strands in the hybrids and the occurrence of similar strands in sterile tissues of pepper plants grown under identical conditions indicate that the small, brown strands in the hybrids may have been caused by other agents.

Table 8.—Immunity to *Fusarium lycopersici* in back-crosses of Earliana x Accession 160 to Accession 160 and in self-progenies of back-cross plants with small, brown strands. Columbia, Missouri. 1936 and 1937.

Progeny or Variety	Year	Treatment*	Greenhouse		Field			
			Seedlings	Infected	Sample Net	Infected Number	Calc. Added	Total Suscepts
BC_1	1936	A	73	0	40	2?	2?	5.5?
BC_1	1936	B	73	0	64	2?	0	2.7?
Susceptible varieties	1936	A	872	490	77	77	305	100.0
	1936	B	208	6	227	223	1121	98.2
BC_1—self (1)	1937	D	90	7	...	...	...	7.8
BC_1—self (2)	1937	A	54	6	23	4	4	25.9
BC_1—self (3)	1937	D	41	6	...	...	...	14.6
Bonny Best	1937	D	165	131	...	...	...	79.4
Susceptible varieties	1937	A	423	156	116	116	151	100.0

*Treatment A, plants grown in steamed, infested soil in the greenhouse and inoculated at transplanting.
Treatment B, plants grown in steamed, non-infested soil in the greenhouse and inoculated at transplanting.
Treatment D, plants grown in steamed, infested soil in the greenhouse, cut and examined 100 days from planting.

Seeds from open-pollinated flowers of 3 back-cross plants with small, brown strands, in the progenies from Earliana x Accession 160 (F_1) x Accession 160, were planted in steamed soil infested with Fusarium Isolate F 7 in the greenhouse in 1937. One progeny was inoculated and transplanted in the field; the other 2 were kept in the greenhouse and examined when 100 days old (Table 8). The percentages of suscepts[13] in these 3 progenies (7.8, 14.6, and 25.9) demonstrated that the parent plants were genetically immune.

Comparisons of progenies from plants in other generations with and without these small, brown strands of vascular tissue also indicated that these 2 types were genetically alike (Text page 54). Therefore, such plants, which could be distinguished from those with typical Fusarium infection, were recorded separately in 1937 to 1939 and included in the immune phenotype in the data reported. If there was any reason to doubt the proper classification of a plant, it was included in the susceptible group. This was done to prevent selection of susceptible plants for breeding work. The records on progenies tested in 1936 were completed before the distinction between plants with typical symptoms of infection by *Fusarium lycopersici* and those with the small, brown strands was recognized. Most of these plants were recorded as infected in 1936; therefore, the reported percentages of suscepts in all segregating populations tested that year probably are somewhat higher than the true percentages.

D. Immunity in Back-cross Progenies From Flowers of Hybrids Pollinated With Pollen of Commercial Varieties

1. First Back-cross[14] Progenies.—F_1 hybrids of Accession 160 with Bonny Best, Bison and Earliana (susceptible) were crossed with Bonny Best, Bison, and Oxheart (susceptible), and with Break O'-Day (resistant). Small progenies tested in the greenhouse and field in 1936, an extremely hot and dry year, yielded percentages of suscepts[15] varying from 33.6 to 50.3 (Table 9). A large progeny from the back-cross to Bonny Best, tested in 1937, and smaller progenies from crosses with Bison and Break O'Day, tested in 1937 and 1938, respectively, yielded percentages of suscepts approaching 50 percent (Table 9). The growing seasons in these years were more favorable for growth of tomato plants and for the development of wilt.

The proportions of susceptible and immune plants in progenies tested in 1937 and 1938 differ from a 1:1 ratio by less than 3 standard errors and indicate that immunity and susceptibility depend upon

[13]Suscepts, as used in this paper, indicates the non-immune phenotype in contrast with the immune phenotype. No distinction is made between different degrees of susceptibility.

[14]The term "back-cross", as used in this paper, indicates a cross between a hybrid and a plant of 1 of the parental types, immune or non-immune; it does not indicate a back-cross to the original parent variety.

[15]The term "suscepts" indicates non-immune plants in segregating progenies; differences in the degree of susceptibility were not considered.

the inheritance of a single pair of contrasting factors. The symbols, I (immunity, dominant) and i (susceptibility, recessive), are proposed as symbols for these factors. The crosses yielding the progenies

Table 9.—Immunity in first back-crosses of hybrids of Accession 160 x susceptible varieties to susceptible and resistant commercial varieties. Columbia, Missouri. 1936, 1937 and 1938.

Pedigree*	Year	Greenhouse		Field			Total Suscepts Percent
		Seedlings	Infected	Sample	Infected Number	Calculated Added Suscepts	
(BB x 160) x BB	1936	147	22	62	26	26	50.3±4.1
(BB x 160) x Oxh	1936	93	4	38	12	16	34.4±5.2
(BB x 160) x BD	1936	51	6	35	9	3	35.3±7.0
(Earl x 160) x BD	1936	149	14	106	28	8	33.6±4.1
(BB x 160) x BB	1937	1129	323	569	195	81	53.1±1.5
(BB x 160) x Bis	1937	111	22	52	18	13	47.7±4.7
(Bis x 160) x BD	1938	55	21	31	6	1	50.9±6.7

*The F_1 hybrids are bracketed; pistillate parents precede staminate parents in statements of crosses. The symbols indicate: BB, Bonny Best; 160, Accession 160; Oxh, Oxheart; BD, Break O'Day; Earl, Earliana; Bis, Bison.

discussed above may then be indicated with symbols:

P_1..I/I (immune) x i/i (susceptible)
F_1..I/i (heterozygous immune) x i/i (susceptible)
BC_1..I/i (heterozygous immune)..50 percent;
i/i (susceptible)..50 percent

The variation in percentages of suscepts in the progenies tested in 1936 may indicate genetic differences in the commercial varieties or experimental error encountered in small progenies, genetically alike, tested under conditions unfavorable for growth of tomato plants and for the development of wilt. Since the crosses with Break O'Day were tri-hybrid in respect to reaction to Fusarium (susceptible x immune x resistant), the factors for resistance from Break O'Day should have been heterozygous, unless Accession 160 had some of the same factors. If these factors were recessive, as suggested by White (1924) and by results on F_1 hybrids between resistant and susceptible varieties reported by Higgins (1927, 1931), they should not have interfered with the classification of non-immune plants. Since nearly all plants of resistant varieties used in these experiments were infected, resistance factors from the resistant varieties should have had no effect, even if they were dominant or duplicated in Accession 160. Although it is possible that resistance factors from Break O'Day may have affected the percentages, progenies from crosses with this variety tested in 1936 yielded percentages of suscepts similar to those in progenies from crosses with Oxheart, a susceptible variety. One small progeny from the cross (Bison x Accession 160) x Break O'Day, tested in 1938, yielded 50.9 percent suscepts. The data sug-

gest that the variation is attributable to experimental error and that all of the commercial varieties used as parents were homozygous for non-immunity (i/i).

2. Second Back-cross Progenies.—In 1936, plants free from infection were selected from first back-cross progenies on the basis of desirable characters, particularly size and abundance of fruits. Cuttings of these plants were rooted in sand and potted in steamed soil infested with Fusarium Isolate F 7 in the greenhouse. They were crossed with 4 early-fruiting varieties: Bonny Best and Bison, susceptible; Break O'Day and Louisiana Pink, resistant.

In most combined greenhouse and field tests, some plants were killed by agents other than wilt and a few escaped infection. To eliminate these sources of error, some of the second back-cross progenies were tested in the greenhouse under more accurately controlled conditions than the various progenies included in the regular spring plantings. The seeds were planted in steamed soil, infested with Fusarium Isolate F 7, on January 30, 1937. Accession 160, Bonny Best, Bison, and Louisiana Pink served as checks. Four pots of steamed soil were planted with Ponderosa. When the plants were 22 days old, all of the infested pots and 2 of the pots of Ponderosa were watered with a suspension of the fungus and ½ inch of steamed sand was added to each pot. To eliminate various sources of error, the pots were placed in a mouse-proof, wire cage, on boards sprayed with 6-6-50 Bordeaux mixture. Check pots were separated from infested pots by vertical panes of glass. The temperatures, although slightly low, usually were maintained near the optimum for the development of Fusarium wilt, as determined by Clayton (1923a).

The cumulative percentages of wilt in the greenhouse are presented graphically in Figure 8. Accession 160 yielded entirely healthy plants. The graph indicates the rapid rate of killing of Bonny Best and Bison (susceptible) and the somewhat slower rate of Louisiana Pink (resistant) following soil infestation when the seeds were planted. Ponderosa (susceptible), planted in steamed soil infested when the plants were 22 days old, wilted rapidly and exceeded Louisiana Pink in 50 days (April 11). The 2 treatments were sufficient to kill nearly all plants of susceptible and resistant varieties within 50 days. In contrast to the curves for susceptible and resistant varieties, the curves for the back-cross progenies having hybrids as pistillate parents are very uniform and attain their peaks at approximately 50 percent after 50 days. (Progenies having hybrids as staminate parents are discussed on Text pages 48-51).

The remaining plants were inoculated as they were set in the field during the second week in May. At this time, the plants (3½ months

old) were large and in a starved condition from crowding; some bore half-grown fruits. Because of their size, it was necessary to set the plants deeply (15 to 20 inches). They grew very little during the summer and did not set fruits until late in the season.

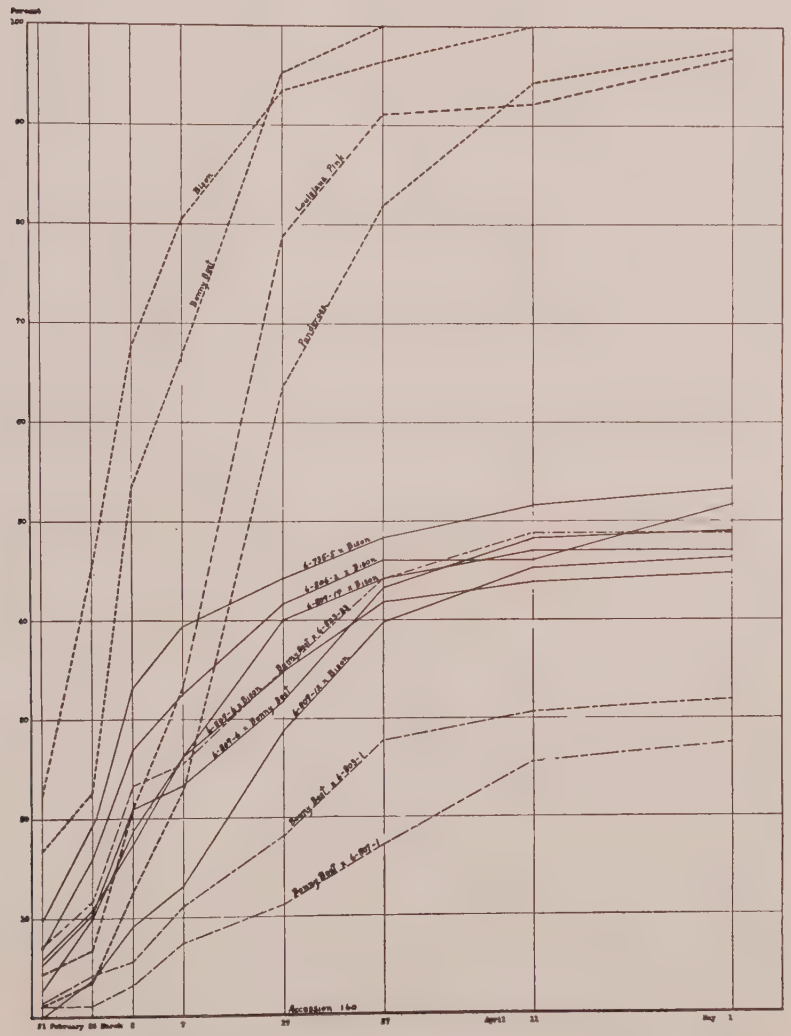

Fig. 8.—Cumulative percentages of wilt in progenies from second back-crosses of hybrids to commercial varieties of tomatoes; February to May, 1937. Commercial check varieties are indicated by dotted lines; progenies from fruits produced on hybrids, by solid lines; hybrid progenies from fruits produced on commercial varieties, by broken lines; Accession 160 yielded entirely healthy plants. Greenhouse, Columbia, Missouri.

Although a few plants were killed by other agents, only 4 of 596 plants set in the field developed external symptoms of Fusarium infection and few others had brown strands in the vascular tissues at the end of the season. The combined greenhouse and field data, from January 30 until the end of September, are summarized in Table 10.

The second back-cross progenies from flowers of hybrids between Accession 160 and susceptible varieties pollinated with pollen of susceptible varieties segregated 49.1 ± 1.8 percent suscepts. A similar progeny from a hybrid with both resistant and susceptible varieties in its pedigree segregated 54.8 ± 4.5 percent suscepts indicating the use of the resistant variety, Break O'Day, as a parent once had no effect on the expression of susceptibility.

Table 10.—Immunity to *Fusarium lycopersici* in second back-crosses of selected hybrids to commercial varieties. Greenhouse and field, Columbia, Missouri. January to September, 1937.

Pedigree or Variety*	Treatment†	Greenhouse		Field	Total Suscepts‡ Percent
		Seedlings	Infected	Infected Number	
((S x 160) x S 12) x S	A	196	87	4	46.4±3.6
((S x 160) x S 6) x S	A	395	182	14	49.6±2.5
((S x 160) x S 14) x S	A	115	54	2	48.7±4.7
((S x 160) x S 2) x S	A	89	46	1	52.8±5.3
Total	A	795	369	21	49.1±1.8
((S x 160) x R 2) x S	A	124	66	2	54.8±4.5
S x ((S x 160) x R 3)	A	43	21	2	53.5±7.6
S x ((S x 160) x S 1)	A	98	27	4	31.6±4.7
S x ((S x 160) selfed)	A	74	23	2	33.8±5.5
Accession 160	A	88	0	0	0.0
Accession 160	B	43	0	0	0.0
Bonny Best	A	84	84	..	100.0
Bonny Best	B	89	0	..	....
Bison	A	31	31	..	100.0
Bison	B	33	0	..	....
Louisiana Pink	A	88	87	1	100.0
Louisiana Pink	B	92	0	..	....
Ponderosa	A	88	86	2	100.0
Ponderosa	B	100	0	..	....

*Pistillate parents precede staminate parents in statements of crosses. The inner brackets indicate the F_1 hybrids; the outer brackets, the selections used as parents. S—susceptible varieties, Bonny Best, Bison, Oxheart, Earliana; R—resistant variety, Break O'Day; 160—Accession 160.

†Treatments: A, greenhouse, soil infested; B, greenhouse, soil non-infested.

‡Standard errors calculated on the actual proportions of suscepts.

In addition to the 2 soil infestation treatments in the greenhouse, the hybrids were inoculated as they were set in the field. Since the check plants were nearly universally infected in the greenhouse, other lots of seedlings were grown in infested and non-infested soil during April and May and inoculated at transplanting. Those grown in infested soil became infected to the extents of 100.0 and 98.2 percent in susceptible and resistant varieties, respectively (Table 4). These varieties, subjected to infection only in the field, were 95.5 and 91.7 percent infected in the 2 groups. (Table 4).

Although the second back-cross progenies were subjected to 2 sets of conditions (in the greenhouse and in the field) either of

which killed nearly 100 percent of all commercial varieties, only the expected 50 percent infection occurred (Table 10). In contrast with the resistance of resistant commercial varieties, in which the severity of infection is affected by environmental conditions, the immunity of the heterozygous hybrids was not broken under conditions very favorable for the development of wilt. These data are considered substantial proof that immunity and susceptibility are governed by the inheritance of a single pair of contrasting factors, (I) immunity, dominant and (i) susceptibility, recessive.

Additional progenies from second back-crosses of selected hybrids to commercial varieties were tested in the regular spring plantings for the field in 1937. High temperatures could not be maintained in the greenhouse, and the percentages of killing in resistant and susceptible varieties were correspondingly low (Table 4, Treatment A, Greenhouse). The final percentages of infection in the check varieties which received the same treatments as the hybrids were 98.2 and 100 percent respectively (Table 4, Treatment A, Total).

The second back-cross progenies yielded percentages of suscepts approximating 50 percent (Table 11). The occurrence of the resistant varieties, Break O'Day and Louisiana Pink, 1 time in pedigrees of the hybrids apparently had no effect on the percentages of suscepts. Progenies from crosses in which these varieties were used either in first or second back-crosses yielded approximately the same percentages of suscepts as the progenies from crosses involving only Accession 160 and susceptible varieties. Factors for resistance, if inherited from the commercial parents, were not potent enough to affect the percentages of suscepts in the progenies.

Table 11.—Immunity to *Fusarium lycopersici* in second back-crosses of selected hybrids to commercial varieties of tomatoes. Columbia, Missouri. April to September, 1937.

Pedigree*	Progenies	Greenhouse		Field		Calculated Suscepts	Total Suscepts Percent
		Seedlings	Infected	Sample	Infected		
((S x 160) x S) x S	17	949	153	562	200	78	45.4±1.6
((S x 160) x R) x S	8	417	81	253	93	30	48.9±2.4
((S x 160) x S) x R	2	86	8	52	22	11	47.7±5.4

*Pistillate parents precede staminate parents in statements of crosses; the inner brackets indicate F_1 hybrids; the outer brackets, hybrid parents of the progenies tested. S—susceptible varieties; Bonny Best, Oxheart, Bison, Ponderosa, and Earliana; R—resistant varieties, Louisiana Pink and Break O'Day; 160—Accession 160.

These experiments were not designed to test the occurrence of resistance factors in Accession 160. Plants known to be homozygous for the recessive immunity factor were discarded. In 1938, greenhouse and field tests of a few progenies from susceptible parents that had escaped infection in 1937 yielded various percentages of infected

plants (Table 12). Some of the progenies, particularly those several generations removed from Accession 160, yielded percentages comparable with those of commercial varieties (Tables 12 and 4). Others yielded lower percentages of suscepts. Although these tests were neither numerous nor thorough enough to demonstrate the occurrence of resistance factors in Accession 160, they do support this hypothesis.

Table 12.—Infection by *Fusarium lycopersici* in progenies of 13 susceptible segregates in various progenies of hybrids between Accession 160 and commercial varieties of tomatoes. Columbia, Missouri. 1938.

Pedigree	Progeny*	Greenhouse		Field			
		Seedlings	Infected	Sample	Infected Number	Calc. Added Susc.	Total Suscept Percent
S x ((S x 160) x S)	(1)	52	20	20	15	9	92.3
((S x 160) x S_2) x S	(2)	83	62	21	15	0	92.8
((S x 160) x S_2) x S	(3)	11	8	3	3	0	100.0
((S x 160) x S_2) self	(3)	109	28	73	26	3	52.3
((S x 160) x S x R) self	(4)	49	8	31	19	6	67.3
(R x (S x 160) x S) x S	(5)	42	24	12	7	3	81.0
((S x 160) x R x S_2) self	(6)	52	29	16	16	6	100.0
((S x 160) x R x S_2) x S	(7)	12	4	5	5	3	100.0
((S x 160) x R x S_2) x S	(7)	22	22	...	...	...	100.0
((S x 160) x R x S_2) x S	(8)	100	93	...	...	...	93.0
((S x 160) x R x S_2) self	(9)	118	110	...	...	...	93.2
((S x 160) x R x S_2) self	(10)	209	174	...	...	...	83.3
((S x 160) x R x S_2) self	(11)	110	100	...	...	...	90.1
((S x 160) x R x S_2) self	(12)	98	81	...	...	...	82.7
((S x 160) x R x S_2) x S	(13)	119	112	...	...	...	94.1
((S x 160) x R—self—self x S—self) x S	(14)	71	58	13	2	0	84.5
((S x 160) x S_2) third self	(15)	45	33	12	4	0	82.2
((S x 160) x R x S_2 x R) self	(16)	21	21	...	...	...	100.0
((S x 160) x R x S_2 x R) self	(17)	48	34	14	10	0	91.7
((S x 160) x R x S x R) second self	(18)	49	48	...	...	...	98.0
((S x 160) x R x S_3) second self	(19)	33	22	11	9	0	93.9

*Back-cross progenies duplicate progenies from self-pollinated flowers with the same progeny number, in parentheses. S_2 indicates 2 successive back-crosses to susceptible varieties. Other symbols as in Table 11.

The hypothesis is also supported by observations on susceptible plants in segregating populations. The proportions of the suscepts in segregating progenies killed during the periods in the greenhouse prior to field setting usually lagged behind the proportions in susceptible and resistant commercial varieties. In the field, comparatively large proportions of the suscepts in segregating progenies grew throughout the seasons. Many of them grew quite large and fruited abundantly before showing any external symptoms of the disease (yellowing, dwarfing, and wilting). The possibility that Accession 160 possesses factors for resistance to *Fusarium lycopersici* in addition to the factor for immunity (I) needs further study.

3. Third and Fourth Back-cross Progenies.—Progenies from third and fourth back-crosses of selected hybrids to commercial varieties were tested in 1938. Data on the checks (commercial varieties) indicated that excellent elimination of suscepts occurred in both the greenhouse and field (Table 4).

There was little evidence that the accumulation of genes from susceptible or resistant commercial varieties affected the potency of the

dominant immunity factor (Table 13). Although the proportions of immune and susceptible plants (46.7 and 53.3 ± 1.0) in progenies from third back-crosses differed from a 1:1 ratio by slightly more than 3 standard errors, the difference probably is attributable to errors in the numbers of calculated suscepts among plants discarded and lost. The percentage of suscepts (49.3 ± 1.8) in the fourth back-cross progenies did not differ from the percentage expected if immunity is dependent on a single, dominant, genetic factor unaffected by modifying genes.

Table 13.—Immunity to *Fusarium lycopersici* in third and fourth back-crosses to commercial varieties. Greenhouse and field, Columbia, Missouri. 1938. S—susceptible variety; R—resistant variety.

Pedigree	Progenies	Greenhouse		Field		Calc. Added Susc.	Total Suscepts Percent*
		Seedlings	Infected	Sample	Infected Number		
((S x 160) x S_2) x S	25	986	488	422	48	9	55.3±1.6
((S x 160) x R x S) x S	18	690	358	265	24	6	56.2±1.9
((S x 160) x S x R) x S	1	36	11	21	0	0	30.6±8.3
((S x 160) x S_2) x R	10	332	150	150	17	4	51.5±2.7
((S x 160) x R x S) x R	6	275	114	118	6	2	44.4±3.0
Total, BC_3	60	2319	1121	976	95	22	53.3±1.0
((S x 160) x R x S_2) x S	13	707	311	297	30	10	49.6±1.9
((S x 160) x R x S_2) x R	1	29	9	15	2	1	41.4±9.3
Total, BC_4	14	736	320	312	32	11	49.3±1.8

*Standard errors were calculated on the expected proportion of suscepts, 50 percent.

4. Back-cross Progenies With Complex Pedigrees.—Progenies from back-crosses of various selected hybrids to commercial varieties yielded 2 types of progenies: (1) non-segregating progenies from hybrid parents homozygous for the dominant immunity factor and (2) segregating progenies from heterozygous hybrid parents yielding approximately 50 percent suscepts (Table 14).

Table 14.—Tests of hybrids from back-crosses of various selected hybrids to commercial varieties. 1938 and 1939.

Pedigree	Progenies	Greenhouse		Field		Calc. Added Susc.	Total Suscepts Percent*
		Seedlings	Infected	Sample	Infected Number		
((S x 160) x R—self x S) x S							
Segregating	6	365	145	161	13	5	44.7±2.6
((S x 160) x R—second self) x S							
Segregating	3	241	113	111	4	1	49.0±3.2
((S x 160) x R x S—second self x S							
Segregating	1	36	17	19	1	0	50.0±8.3
((S x 160) x R x S x S—self) x S							
Segregating	1	49	28	20	0	0	57.1±7.1
Homozygous	1	47	0	47	0	0	0.0
((S x 160) x R x S_2—second self) x S							
Segregating	2	89	43	46	8	0	57.3±5.2
((S x 160) x R x S_3—self) x S							
Segregating	2	60	18	41	1	0	31.7±6.0
Homozygous	1	48	0	48	0	0	0.0
((S x 160) x R—self x S—second self) x S							
Homozygous	1	34	0	34	0	0	0.0
Total, segregating	15	840	364	398	33	6	47.3±1.7
Total, homozygous	3	129	0	129	0	0	0.0

*Standard errors were calculated on the actual percentages of suscepts.

5. Discussion.—Genetic factors from commercial varieties may have acted in progenies from successive back-crosses in 2 ways: (1) modification of the expression of the recessive immunity factor in the non-immune (i/i) genotype; (2) modification of the expression of the dominant immunity factor in the immune (I/i) genotype. Factors present in the resistant commercial varieties apparently cause modifications of the first type; these varieties are homozygous for non-immunity. Such factors, if effective in populations segregating immune and non-immune plants, would cause some of the non-immune plants to be misclassified, resulting in proportions of immune plants exceeding the true proportions. Such factors from the commercial varieties used in these crosses could have had little effect because (a) commercial resistant varieties treated like the hybrids were infected to the extent of 96.1 percent or more each year; and (b) the resistant varieties occurred as parents but once in the pedigrees of most of the hybrids. The factors would have to be dominant or duplicated in Accession 160 to be effective in these hybrids. The work of White (1924) and Higgins (1927, 1931) indicated that the factors were recessive in some resistant varieties. With the possible exception of the first back-crosses the data were not affected by these factors. Second, third, and fourth back-crosses yielded approximately equal proportions of immune and susceptible plants. The proportions were not affected by the use of resistant or susceptible commercial varieties as parents.

Factors from commercial varieties affecting the expression of the dominant immunity factor in the immune (I/i) genotype would cause some of these plants to be mis-classified, resulting in a decrease of the obtained from the expected proportion of immune plants. Such factors could be the allels of the factors discussed above, or other modifying factors. The effectiveness of such factors would increase in successive back-crosses because of increases in homozygosity. The data show that the effectiveness of the dominant immunity factor, I, was not decreased by the accumulation of genes from commercial varieties in successive back-cross progenies.

E. Immunity in Back-cross Progenies From Flowers of Commercial Varieties Pollinated with Pollen From Hybrids

Back-cross progenies from flowers of commercial varieties pollinated with pollen of selected hybrids segregated differently from back-cross progenies from the reciprocal crosses discussed on text pages 42-47. Four progenies from Break O'Day pollinated with pollen of F_1 hybrids yielded proportions of suscepts smaller than progenies from the reciprocal crosses (Table 15). Although the progenies were

too small to yield statistically significant differences individually, under the conditions of the experiment, all of the progenies varied in the same direction. The difference between the totals for similar progenies (12.0 ± 3.9) suggested that the direction of crossing affected the percentages. In 1 small progeny from Bonny Best pollinated with pollen from the F_1 hybrid, tested in 1937, the proportions of suscepts (21.7 ± 4.5 percent) and immune plants (78.3 ± 4.5 percent) differed from a 1:1 ratio by more than 6 standard errors (Table 15). The difference between these proportions and the proportions in progenies from the reciprocal cross (53.1 ± 1.5 and 46.9 ± 1.5 percent) tested under identical conditions is more than 6 times its standard error (31.4 ± 4.8) and, therefore, significant. Although several plants in the aberrant progeny were killed by agents other than *Fusarium lycopersici*, it does not seem likely that an exceptionally large proportion of these plants was susceptible. It would be necessary to assume that 24 of the 29 discarded and lost plants were susceptible to make the proportions (21.7 and 78.3) equal to those in progenies from the reciprocal cross.

Table 15.—Immunity in reciprocal first back-crosses of selected hybrids to commercial varieties. Greenhouse and field; Columbia, Missouri.

Pedigree*	Year	Treatment†	Greenhouse		Field			Total Suscepts Percent
			Seedlings	Infected	Sample	Infected Number	Calc. Added Susc.	
BD x (BB x 160)	1936	A	138	0	87	26	15	29.7±3.9
BD x (Earl x 160)	1936	A	161	5	138	30	4	24.2±3.4
(BB x 160) x BD	1936	A	51	6	35	9	3	35.3±6.7
(Earl x 160) x BD	1936	A	149	14	106	28	8	33.6±3.5
BD x (BB x 160)	1936	B	39	0	29	7	2	23.1±6.7
BD x (Earl x 160)	1936	B	37	0	35	14	1	40.5±8.1
(Earl x 160) x BD	1936	B	37	0	23	10	6	43.2±8.2
BB x (BB x 160)	1937	A	83	7	47	7	4	21.7±4.5
(BB x 160) x BB	1937	A	1129	323	569	195	81	53.1±1.5

*F_1 hybrids are bracketed; pistillate parents precede staminate parents in statements of crosses. Symbols indicate: BD, Break O'Day; BB, Bonny Best; 160, Accession 160; Earl, Earliana.
†Treatment: A, plants grown in infested soil in the greenhouse and inoculated at transplanting; B, plants grown in non-infested soil in the greenhouse and inoculated at transplanting.

Two progenies from Bonny Best pollinated with pollen of first back-cross selections and 1 from Bonny Best pollinated with pollen from an F_2 selection were tested under particularly favorable conditions in 1937 (Text pages 42-45). The data are included in Table 10 and represented graphically in Figure 8. The curves for 2 of these progenies are distinctly different from those for progenies from reciprocal crosses. These progenies ultimately yielded 31.6 ± 4.7 and 33.8 ± 5.5 percent suscepts with a total of 32.5 ± 3.6. The difference between this percentage and the percentage of suscepts in progenies from comparable reciprocal crosses (49.1 ± 1.8 percent) is

16.6 ± 4.0 and indicates that these 2 progenies differed genetically from progenies from the reciprocal crosses. The third progeny, from the cross Bonny Best♀ x ((Bonny Best x Accession 160) x Break O'Day)♂ segregated 53.5 ± 7.6 percent suscepts, and did not differ significantly from the progeny from the reciprocal cross (54.8 ± 4.5 percent suscepts). The curve representing cumulative percentages of wilt in the greenhouse was similar to the curve for the reciprocal cross (Figure 8).

The differences in percentages of suscepts in progenies from flowers of commercial varieties pollinated with pollen of hybrids and in progenies from reciprocal crosses indicate that the factor for immunity is linked in inheritance with a factor affecting the development or effectiveness of the microgametophyte or the microgamete. Genes affecting the microgametophyte generation of the tomato have been reported by Crane (1915) and Lesley and Lesley (1939). The part of the life cycle directly affected by this factor is interesting, but not essential to a genetic analysis of the data on immunity and susceptibility to Fusarium wilt. The end result, so far as these data are concerned, is a difference in the effectiveness, in fertilization, of microgametes bearing the contrasting allels. Since these genes affect the haploid generation, no dominance is indicated. The symbol X is arbitrarily selected to indicate a genetic factor favorable to effectiveness of microgametes bearing it; the symbol x indicates the allel which tends to prevent fertilization by gametes bearing it *in competition with gametes bearing X*. Since plants homozygous for x set fruits readily, the factor x does not prevent fertilization by microgametes bearing it if these are not competing with X-bearing gametes; it is not a lethal factor.

Fruit setting and seed development occurred in Accession 160 during periods of drought and high temperatures that inhibited fertilization in the commercial varieties. It is possible that the X factor was responsible for fertilization in this accession under these conditions. Pollinations with pollen of hybrids during such periods may have resulted in higher percentages of seeds developed after fertilization of megagametes by X-bearing microgametes than pollinations during periods when conditions were more favorable for fruit setting in the commercial varieties. Since seeds used in these experiments were not collected from fruits set under identical conditions, some variation may be expected in percentages of suscepts in different progenies.

If the 2 allelomorphic genes, X and x, with the properties described above, do exist, the data on all progenies from flowers pollinated with pollen of hybrids yield to analysis. If Accession 160 is

homozygous for X as well as for I (immunity) and the commercial varieties are homozygous for x as well as for i (non-immunity), then F_1 hybrids are heterozygous for both factors (X/x, I/i).

If the factors X and I were on different pairs of chromosomes, independent assortment at meisosis would result in the production of 4 classes of microspores in equal proportions: (XI), (Xi), (xI), and (xi). Since the 4 combinations in the microspores, and therefore in the microgametophytes and microgametes, would be equal, the factors X and x would have no effect upon the percentages of immune and nonimmune offspring. It was only through linkage with the genes for immunity and non-immunity that the effects of the X and x factors were measured in the experiments.

If the genes X and I are on the same chromosome, the genotype of the F_1 hybrids should be (XI) (xi) and the numbers of microgametes with these combinations, (XI and (xi), should exceed those with the cross-over combinations, (Xi) and (xI). Therefore, first back-cross progenies from flowers pollinated with pollen from F_1 hybrids should have proportions of immune plants exceeding 50 percent, expected on the basis of single factor inheritance. Back-crosses from flowers of F_1 hybrids pollinated with pollen of commercial varieties should yield the expected proportion of 50 percent suscepts, since the commercial varieties are homozygous for x and the X/x factors have no effect on megagametophyte or megagametes. The first back-cross progenies did yield these results. (Text pages 40-42).

If the hypothesis is true, second back-cross progenies from flowers of commercial varieties pollinated with pollen of first back-cross selections should be of 2 types. The immune first back-cross parents would have the (xi) combination from the susceptible parent and the (XI), non-cross-over, or (xI), cross-over, combination from the hybrid parent and would have 2 possible genotypes (XI)(xi) and (xI)(xi). Those with the (XI)(xi) genotype would yield second back-cross progenies with more than 50 percent immune plants; those with the (xI) (xi) genotype would yield progenies with 50 percent suscepts. Of 3 progenies from flowers of commercial varieties pollinated with pollen of first back-cross and F_2 selections, 2 yielded 31.6 and 33.8 percent suscepts, indicating that the hybrid parents had the (XI)(xi) combination; the third yielded 53.5 percent suscepts, indicating that the hybrid parent had the (xI)(xi) genotype.

The occurrence of 1 progeny from a cross-over parent among the 3 second back-cross progenies tested indicates that crossing-over between X and I may occur frequently. The proportions of immune and susceptible plants in the progenies from parents with the (XI)

(xi) genotype indicate that the percentage of crossing-over is less than 33 percent. If only X-bearing microgametes were effective in fertilization, the percentage of suscepts in these progenies (32.6) would equal the percentage of crossing-over. Since x-bearing gametes were effective in some degree and non-cross-over (xi) gametes would be produced in larger numbers than cross-over (xI) gametes, the x-bearing gametes would tend to increase the proportions of suscepts in the progenies, and therefore, to increase the apparent percentage of crossing-over. Since the portion of suscepts resulting from fertilization by (xi) gametes could not be determined directly, and no progeny tests were made, the exact percentage of crossing-over could not be determined.

The hypothesis that the factor for immunity is linked with a factor influencing effectiveness of microgametes may be applied to data on other progenies from flowers pollinated with pollen of hybrids.

F. Immunity in F_2 Progenies

F_2 progenies from self-pollinated flowers of F_1 hybrids of Accession 160 with Bonny Best were tested in 1937. Susceptible varieties grown under comparable conditions were 100.0 percent infected (Table 4).

The F_2 progenies, containing 437 plants, yielded 9.6 ± 1.4 percent suscepts. It is possible that resistance factors from Accession 160 prevented the proper classification of some homozygous susceptible segregates. However, it is unlikely that such factors were entirely responsible for the low percentage of suscepts obtained.

The hypothesis that the immunity factor is linked with a factor influencing the effectiveness of the microgamete provides a more probable explanation of the behavior of the F_2 progenies. The classes expected on selfing plants with the (XI)(xi) genotype are shown in Table 16.

The shaded half of the table represents the combinations that are reduced in frequency if x microgametes function less frequently than X microgametes. The X and x factors apparently have no effect on the megagametophyte or megagamete, since progenies from crosses in which hybrids are used as pistillate parents yield proportions of suscepts expected on the basis of single factor inheritance.

The letters l and m indicate the frequencies of the classes of gametes; l will equal m in the absence of linkage and will exceed m if X and I are linked, the degree depending on the intensity of linkage.

With no linkage the proportion of susceptible plants will be 25 percent regardless of the extent to which x affects the functioning of the male gametes.

Table 16.—Diagram of the relative frequency of production of F_2 zygotes from crosses between Accession 160 (XI) (XI) and commercial varieties (xi) (xi).

♀ \ ♂	l XI	m Xi	m xI	l xi
l XI	l^2 $\frac{XI}{XI}$	lm $\frac{Xi}{XI}$	lm $\frac{xI}{XI}$	l^2 $\frac{xi}{XI}$
m Xi	lm $\frac{XI}{XI}$	m^2 $\frac{Xi}{XI}$	m^2 $\frac{xI}{XI}$	lm $\frac{xi}{XI}$
m xI	lm $\frac{XI}{xI}$	m^2 $\frac{Xi}{xI}$	m^2 $\frac{xI}{xI}$	lm $\frac{xi}{xI}$
l xi	l^2 $\frac{XI}{xI}$	lm $\frac{Xi}{xI}$	lm $\frac{xI}{xI}$	l^2 $\frac{xi}{xI}$

With linkage the frequency of susceptible plants will be reduced, but the degree of reduction will depend on both the intensity of linkage between X and I and the relative efficiencies of X-bearing and x-bearing microgametes. The only F_2 plants derived from gametes favored by the X factor and present in larger numbers because they contain non-cross-over combinations are in the immune phenotype. The only susceptible plants are those derived (1) from gametes produced in smaller numbers because of crossing-over (2) from gametes handicapped by the presence of the x factor, or (3) from gametes produced in smaller numbers and also containing the x factor.

The low percentage of suscepts (9.6 ± 1.4) in F_2 progenies suggests that gametes bearing the recessive immunity factor, i, function less frequently than gametes bearing the dominant immunity factor,

I, supporting the hypothesis that I is linked with X, a factor influencing the effectiveness of the microgametophyte.

G. Immunity in F_3 Progenies

The F_3 data are of interest particularly in connection with the effects of linkage between the immunity factor (I) and the gametophyte factor (X). The 16 gene-combinations in F_2 progenies shown in Table 16 may be grouped in 5 classes according to the proportions of suscepts they may be expected to yield in F_3 progenies:

Gene-combinations	Progenies
(1) 1 (XI) (XI), 2 (XI) (xI), 1 (vI) (xI)	immune
(2) 2 (XI) (Xi), 2 (xI) (xi)	25 percent suscepts
(3) 2 (XI) (xi)	less than 25 percent suscepts
(4) 2 (Xi) (xI)	more than 25 percent suscepts
(5) 1 (Xi) (Xi), 2 (Xi) (xi), 1 (xi) (xi)	susceptible

Progenies from 39 non-infected F_2 plants from one F_1 plant were tested in 1938. The progenies were small, averaging 35 plants. One progeny from an infected F_2 segregate was included in the test; it was 80.0 percent infected. Susceptible and resistant varieties were 100.0 and 96.1 percent infected, respectively.

The percentages of suscepts indicated that 15 of the 39 immune parents were homozygous (I/I) and 24 were heterozygous (I/i). The segregating progenies yielded percentages of suscepts varying from 5.6 to 28.6 with a weighted average of 13.5 based on the total of 816 seedlings. Although the number of progenies and the numbers of plants in the progenies were too small to permit an exact analysis, the large proportion of immune progenies, the low percentage of suscepts in segregating progenies, and the variation in percentages of suscepts in different progenies can be explained by incomplete linkage between the factors X and I.

Seeds from several non-infected F_2 plants with comparatively large fruits and from a few small-fruited F_2 plants with small discolored strands of vascular tissue were planted in 1937. A few of the progenies were set in the field; the others were kept in the greenhouse until the plants were 100 days old.

Progenies of 2 infected F_2 plants that did not wilt served as checks in the greenhouse. These 2 progenies were 75.9 and 76.7 percent infected, indicating some suscepts in segregating progenies escaped infection. Resistant commercial varieties were 98.2 percent infected in the field. (Table 4).

The progenies from plants with small, brown strands and those with no discoloration reacted alike, and may be classified into 2 groups: 7 progenies with no infected plants and 50 progenies with

proportions of suscepts varying from 3 to 55 in a nearly continuous series (Table 17). The proportion of immune parents was considerably smaller than would be expected if selection had no effect, suggesting that the genes for immunity and microgamete effectiveness may be linked with factors affecting the size of the fruit.

The 50 segregating progenies may be divided into 3 groups: (1) those from (XI)(xi) parents segregating less than 25 percent suscepts; (2) those from (XI)(Xi) and (xI)(xi) parents segregating approximately 25 percent suscepts; and (3) those from (xI)(Xi) parents segregating more than 25 percent suscepts. Although the series is nearly continuous in F_3 progenies from the cross of Bonny Best with Accession 160, there are gaps between 34 and 43 percent and between 15 and 19 percent. These gaps are more apparent in the F_3 progenies from the cross of Earliana with Accession 160 (Table 17). If the series from both crosses are combined and divided into 3 groups with the limits suggested, there are 7 progenies in the "high" group with an average of 45.4 percent suscepts, 17 in the "medium" group with an average of 25.5 percent suscepts, and 26 progenies in the "low" group with an average of 9.4 percent suscepts.

The difference (30.9 $\pm$ 3.9) between the percentages of infected plants in the 7 progenies in the high group (45.4 $\pm$ 2.2) and in the 2 progenies from infected parents (76.3 $\pm$ 3.2) is nearly 8 times its standard error and indicates these 7 progenies do not belong in the susceptible group. They probably were obtained from F_2 plants which had received 2 cross-over combinations, (Xi)(xI). Although the proportion of these progenies suggests a fairly high percentage of crossing-over between X and I, it is distorted by the selection of 57 immune plants, mostly with large fruits, from a total population of 2350 individuals.

It is probable that the numbers of progenies in the "medium" and "low" groups also were affected by selection, and that several factors affected the percentages of infected plants in the progenies. The fruits were not collected at the same time and it is possible that the advantage of X-bearing gametes over x-bearing ones varies under different conditions. The numbers of plants in the progenies were small, and the percentage of infected plants in the checks indicated that some non-immune plants were not infected. In spite of these sources of error, the proposed grouping includes 26 of the 50 segregating progenies in the "low" group, from parents that had received 2 non-cross-over combinations, (XI)(xi); 17 in the "medium" group, from parents that had received 1 cross-over and 1 non-cross-over combination, (XI)(Xi) and (xI)(xi); and 7 in the

Table 17.—Immunity to *Fusarium lycopersici* in F_3 progenies from crosses of Accession 160 with Earliana and Bonny Best. Columbia, Missouri. 1937.

Cross P_1	Greenhouse		Field			
	Seedlings	Infected	Sample Number	Infected Number	Calculated Added Suscepts	Total Infected Percent
BB x 160	68	0	49	0	0	0
BB x 160	100	0	62	0	0	0
BB x 160	100	0	41	0	0	0
BB x 160	100	0	..	..	..	0
BB x 160	110	0	..	..	..	0
Earl x 160	78	0	61	0	0	0
Earl x 160	50	0	..	..	..	0
BB x 160	51	28	..	..	..	55
BB x 160	72	35	..	..	..	49
BB x 160	98	44	..	..	..	45
BB x 160	86	38	..	..	..	44
BB x 160	82	36	..	..	..	44
BB x 160	99	43	..	..	..	43
BB x 160	64	22	..	..	..	34
BB x 160	100	31	..	..	..	31
BB x 160	100	31	..	..	..	31
BB x 160	97	29	..	..	..	30
BB x 160	101	29	..	..	..	29
BB x 160	96	26	..	..	..	27
BB x 160	90	23	..	..	..	26
BB x 160	101	26	..	..	..	26
BB x 160	98	24	..	..	..	25
BB x 160	100	24	..	..	..	24
BB x 160	95	21	..	..	..	22
BB x 160	100	21	..	..	..	21
BB x 160	62	7	34	4	2	21
BB x 160	105	21	..	..	..	20
BB x 160	100	19	..	..	..	19
BB x 160	114	17	..	..	..	15
BB x 160	94	13	..	..	..	14
BB x 160	99	13	..	..	..	13
BB x 160	68	6	..	..	..	9
BB x 160	74	6	..	..	..	8
BB x 160	87	5	..	..	..	6
BB x 160	90	5	..	..	..	6
BB x 160	73	4	..	..	..	6
BB x 160	136	6	..	..	..	4
BB x 160	91	1	34	1	2	4
Earl x 160	47	19	..	..	..	40
Earl x 160	76	20	..	..	..	26
Earl x 160	56	13	..	..	..	23
Earl x 160	94	15	..	..	..	16
Earl x 160	105	16	..	..	..	15
Earl x 160	96	13	..	..	..	14
Earl x 160	92	12	..	..	..	13
Earl x 160	79	10	..	..	..	13
Earl x 160	118	11	76	3	1	13
Earl x 160	94	11	..	..	..	12
Earl x 160	98	10	..	..	..	10
Earl x 160	90	9	..	..	..	10
Earl x 160	94	9	..	..	..	10
Earl x 160	87	7	..	..	..	8
Earl x 160	94	6	..	..	..	6
Earl x 160	81	5	..	..	..	6
Earl x 160	93	3	..	..	..	3
Earl x 160	98	3	..	..	..	3
Earl x 160	65	2	..	..	..	3
High group (7 prog.)	535	..	..	..	..	45.4
Med. group (17 prog.)	1541	..	..	..	..	25.5
Low group (26 prog.)	2404	..	..	..	..	9.4
Immune (7 prog.)	606	..	..	..	..	0.0

"high" group, from parents that had received 2 cross-over combinations (Xi)(xI).

H. Immunity in First, Second, and Third Selfed Generations

First, second, and third self-progenies of immune selections in populations from second and third back-crosses and from selections

Table 18.—Immunity in first, second, and third self-progenies from back-cross selections. Greenhouse and field, Columbia, Missouri. 1939. S, susceptible; R, resistant; 160, Accession 160.

Pedigree of Back-cross	Progenies Number	Seedlings* Number	Total Infected Percent
	First Self-progenies		
((S x 160) x S x S x S)	26	1054	16.7
((S x 160) x R x S x S)	22	842	15.1
((S x 160) x R x S x R)	8	300	10.7
((S x 160) x R x S x S x S)	18	744	11.1
((S x 160) x R x S x S x R)	3	119	9.2
((S x 160) x R—self x S x S)	18	808	17.8
((S x 160) x R—self—self x S)	7	288	12.8
Totals	102	4155	14.7
	Second Self-progenies		
((S x 160) x S x S)			
(Segregating)	12	466	6.2
(Non-segregating)	2	85	0.0
((S x 160) x R x S)			
(Segregating)	8	297	10.4
(Non-segregating)	5	188	0.0
((S x 160) x S x S x S)			
(Segregating)	14	571	10.2
(Non-segregating)	6	236	0.0
((S x 160) x R x S x S)			
(Segregating)	11	432	11.3
(Non-segregating)	6	256	0.0
((S x 160) x R x S x R)			
(Segregating)	1	36	5.6
(Non-segregating)	1	42	0.0
((S x 160) x R x S x S x S)			
(Segregating)	8	337	11.3
(Non-segregating)	8	340	0.0
((S x 160) x R x S x S x R)			
(Non-segregating)	3	128	0.0
((S x 160) x R—self x S x S)			
(Segregating)	4	176	13.6
(Non-segregating)	3	107	0.0
((S x 160) x R—self x S)			
(Segregating)	4	165	6.7
(Non-segregating)	2	68	0.0
((S x 160) x R—self—self x S)			
(Segregating)	5	200	13.5
Totals			
(Segregating)	67	2680	10.0
(Non-segregating)	36	1450	0.0
	Third Self-progenies		
((S x 160) x S x S)			
(Non-segregating)	4	156	0.0
((S x 160) x R x S)			
(Segregating)	4	150	10.7
(Non-segregating)	7	316	0.0
((S x 160) x R x S x S)			
(Segregating)	5	218	3.2
(Non-segregating)	4	165	0.0
((S x 160) x R—self x S)			
(Segregating)	1	45	15.6
(Non-segregating)	2	75	0.0
Totals			
(Segregating)	10	413	7.3
(Non-segregating)	17	712	0.0

*Seedlings grown in infested soil in the greenhouse and inoculated when transplanted in the field.

with more complex pedigrees segregated proportions of suscepts in accord with the hypothesis that the immunity factor (I) is linked in inheritance with a factor (X) influencing the effectiveness of the microgamete (Table 18). The conditions under which these progenies were tested were very favorable for the growth of tomato plants and for the development of wilt. Resistant and susceptible check varieties grown one month in the greenhouse in infested soil wilted to the extent of 64.7 and 79.1 percent, respectively. These varieties, grown in non-infested soil in the greenhouse and inoculated at transplanting, wilted 100 percent before the end of the season (Table 4). The hybrid progenies were grown in infested soil in the greenhouse and inoculated at transplanting. The data on the check varieties indicates that few, if any, susceptible hybrids escaped infection. So few plants were killed by agents other than Fusarium that there were no added suscepts. Therefore, only the numbers of seedlings and the actual percentages of infected plants are reported.

The low percentages of suscepts in all families of first self-progenies indicate that X was retained in many of the back-cross selections (Table 18). Since commercial varieties usually were used as pollen parents in back-crossing, the X factor was not favored by breeding methods. Most of the plants in generations obtained by continuous back-crossing would be expected to be homozygous for x. However, the practice of selecting prolific, immune plants overbalanced the tendency to lose X because of the effect of X on fertility and linkage between X and I.

According to the hypothesis, a back-cross selection would receive the (xi) combination from its commercial parent and either the (XI) or (xI) combination from its hybrid parent. The back-crosses should be of 2 types: (1) (XI)(Xi) and (xI)(xi) yielding first self-progenies with approximately 25 percent suscepts, and (2) (XI)(xi) yielding progenies with lower percentages.

The self-progenies from back-crosses yielded percentages of suscepts varying from 0 to 42 percent in a nearly continuous series (Table 19). Two maxima occurred at 5 and 17 percent. The wide variation and the failure of the progenies to occur in 2 sharply defined classes probably resulted from 3 causes: (1) Small numbers of individuals (30 to 54) in the progenies, (2) variation in the relative efficiencies of X-bearing and x-bearing microgametes in different gene complexes and under different conditions, (3) failure of infection in some suscepts.

The second and third self-progenies yielded interesting results. Selected parents in first and second self-progenies should be of 4 types: (1) (-I)(-I) homozygous immune yielding non-segregating

Table 19.—Frequency distribution of first, second, and third self-progenies from back-cross selections, based on the percentages of suscepts. Columbia, Missouri. 1939.

Suscepts Percent	First Self-progenies Number	Second Self-progenies Number	Third Self-Progenies Number
0	4	38	17
1-3	12	18	4
4-6	13	14	4
7-9	12	6	..
10-12	7	6	..
13-15	9	7	..
16-18	13	3	1
19-21	9	5	..
22-24	5	1	..
25-27	6	1	..
28-30	2	2	..
31-33	4	..	1
34-36	1	..	..
37-39	4	..	..
40-42	1	1	..
43-45	..	1	..
Totals	102	103	27

progenies, (2) (XI)(xi) yielding low percentages of suscepts, (3) (XI)(Xi) and (xI)(xi) yielding 25 percent suscepts, (4) (xI)(Xi) yielding high percentages of suscepts. Since the X factor was favored in breeding (successive self-pollinations) as well as by selection, the majority of the second and third self progenies would be expected to occur in the first 2 classes. The numbers of progenies in the third class would be reduced by linkage between X and I and natural and artificial selective discrimination against plants homozygous for x. The fourth class with high percentages of suspects would be expected to occur occasionally in second self-progenies because they would be derived from first self-parents that had received 2 cross-over combinations.

Failure to obtain definite classes in the second self-progenies probably resulted from the 3 causes mentioned on Text page 58 and from the small numbers of progenies (Table 19). Most of these progenies segregated none or very few suscepts. There were not enough progenies in the other 2 classes to establish modes for the classes. Two progenies, yielding 41 and 45 percent suscepts, apparently were derived from parents with the (Xi) (xI) combination.

Twenty-seven third self-progenies included 17 with no suscepts, 8 with 2 to 6 percent suscepts, and 2 with 17 and 31 percent. It is probable that these represent 3 of the 4 possible classes of progenies. The fourth class, with high percentages of suscepts should occur but rarely in advanced generations unless a parent is selected from a progeny with a high percentage of suscepts.

The tendency of successive self-progenies from back-crosses to occur in the immune class and the "low" segregating class is indicated in the frequency distributions of the first, second, and third self-progenies listed in Table 19, and the successively lower total per-

centages of suscepts in segregating progenies in the 3 generations (Table 18).

The large number of homozygous immune progenies in second and third self-generations and the percentages of suscepts in the segregating progenies in the 3 successive self-generations support the hypothesis (Text page 48) that the accumulation of genes from commercial varieties has no effect on the expression of the dominant immunity factor, I.

I. Discussion

The validity of the hypothesis that a gene, X, linked with I, influences the effectiveness of the microgamete is supported by the occurrence of segregating progenies in different classes based on the percentages of suscepts. (1) Progenies of F_1 hybrids pollinated with pollen from commercial varieties yielded approximately 50 percent suscepts; reciprocal crosses yielded progenies with lower percentages of suscepts. (2) Second back-crosses from hybrids pollinated with pollen from commercial varieties yielded 50 percent suscepts; progenies from the reciprocal crosses yielded 2 types of progenies, (a) segregating 50 percent suscepts and (b) segregating lower percentages of suscepts. (3) F_2 progenies, from the original cross between Accession 160 and Bonny Best yielded low percentages of suscepts. (4) Segregating F_3 progenies were of 3 types: (a) yielding 25 percent suscepts, (b) yielding lower percentages, (c) yielding higher percentages.

Classes in small progenies in successive self-generations from back-cross selections were not well defined. First self-progenies from selected hybrids yielded percentages of suscepts varying from 0 to 42 with maxima at 5 and 17 percent. Most of the second self-progenies were immune or segregated small percentages of suscepts; a few yielded percentages approaching 25, and 2 yielded large percentages. A few third self-progenies included 3 of the 4 possible classes: 17 progenies were homozygous immune; 8 segregated 2 to 6 percent suscepts; and 2 segregated 17 and 31 percent suscepts.

The data from all progenies can be interpreted on the basis of the hypothesis that a gametophyte factor, X, is linked with I, and the evidence from all sources is considered substantial support of the hypothesis.

The data on percentages of wilt and infection in segregating populations and observations on fruit setting in the parent varieties indicate that the X factor governs, at least in part, a second valuable and interesting character found in *Lycopersicon pimpinellifolium* Accession 160, namely, fecundity superior to that in several commercial

varieties of *L. esculentum* under the environmental conditions encountered in these experiments.

10. PROGRESS IN DEVELOPING IMMUNE VARIETIES

The objective of the breeding program has been to develop an early, prolific tomato with a long fruiting period, medium-large, oval fruits of desirable shape and quality, stocky stems, well-branched habit of growth, and immunity to *Fusarium lycopersici.*

Fig. 9.—Fruit specimens from the tomato wilt test plot, University South Farms, Columbia, Missouri, 1938. A, ((Bonny Best x Accession 160) x Oxheart x Bison) self, 90 grams; B. ((Earliana x Accession 160) x Break O'Day x Bonny Best x Oxheart), 160 grams; C, ((Bonny Best x Accession 160) x Oxheart x Louisiana Pink x Bonny Best), 100 grams.

Many of the immune plants in the second, third and fourth backcross progenies were similar in many characters to the commercial varieties of *Lycopersicon esculentum* (Figure 9). It is apparent that the gene for immunity is as potent in combination with many genes of commercial varieties as in the gene complex of *L. pimpinellifolium*

Accession 160. It appears certain, therefore, that a tomato with desirable plant and fruit characters and homozygous for immunity can be produced. It is reasonable to believe that tomato varieties combining the desired plant and fruit characters with immunity to Fusarium wilt can be developed by selection among selfed lines of the hybrids.

A. Methods

Since the objective of the breeding program was to combine immunity from Accession 160, dependent upon a single dominant factor, with many plant and fruit characters from commercial varieties the greatest emphasis was placed on successive back-crosses to commercial varieties. This method was of value, also with respect to fruit size. Groth (1914, 1915), Frimmel (1922), Myers (1924), and others have demonstrated that fruit size in the tomato depends upon multiple factors, and the work of Lindstrom (1926a, 1926b, 1928, 1932), MacArthur (1935), Butler (1937), Yeager (1937), MacArthur and Butler (1938), and Powers (1939b) has indicated that several, if not all, of the chromosomes have factors affecting this character. Earliana and Bonny Best were used for the first generation hybrids. Since both have relatively small fruits and the very small fruits of Accession 160 ($\pm$ 1.0 gram) seemed to be a difficult obstacle to the breeding program, various other varieties were used for crossing in later generations. These varieties included Bison, Break O'Day, Early Baltimore, Greater Baltimore, Louisiana Pink, Oxheart, Ponderosa, White Beauty, and Yellow Ponderosa.

Since many of these varieties, particularly those with large fruits had various undesirable characters, they were not used repeatedly in back-crosses. Instead, back-crosses to susceptible and resistant commercial varieties were subjected to selection under field conditions. Since nearly all plants of resistant varieties were infected, and crosses involving resistant varieties segregated approximately the same proportions of suscepts as crosses involving only Accession 160 and susceptible varieties, it is apparent that the use of resistant varieties did not interfere with the elimination of non-immune plants.

Lycopersicon pimpinellifolium Accession 160 has, in addition to immunity to *Fusarium lycopersici,* some other characters that would be of value in a commercial tomato variety. One of these is more effective fertilization resulting from the influence of the X factor on the effectiveness of the microgamete. Other desirable characters of this accession are earliness, fecundity, and probable resistance to adverse environmental conditions and some diseases other than wilt.

In an attempt to maintain some of the desirable characters of Ac-

cession 160, some lines were obtained by a program of selfing and back-crossing to commercial varieties, resulting in the complex pedigrees mentioned on Text pages 47 and 57.

To secure desirable characters from Accession 160 and various commercial varieties, the breeding program was combined with field selection. Non-infected plants in the field were selected entirely on the basis of their desirable characters without regard to their pedigrees. As a result, most of the later generations had several commercial varieties in their pedigrees. This is considered an advantage since progenies from self-pollinated flowers of these multi-hybrids may yield segregates with combinations of desirable characters from several commercial varieties and Accession 160.

B. Fruit Size

The elimination of susceptible plants before fruiting prevented a genetic analysis of fruit size and other characters in these progenies. However, some of the data on weight and numbers of locules of fruits of selected plants grown in the field in 1937 indicate the progress made in different generations.

For comparison with the hybrids, various commercial varieties were grown in non-infested soil in the greenhouse and set in a nearby field that had not been used for a tomato crop.

Average weights of fruits of commercial varieties, Accession 160, and a few selected hybrids are presented in Table 20. The average weights of fruits of commercial varieties varied from 62 grams in Break O'Day to 159 grams in Ponderosa, while the currant-like fruits of Accession 160 weighed 1.2 grams. The average weight of 100 fruits of F_1 hybrids between Accession 160 and Bonny Best was 4.8 grams, while the average weight of fruits of F_1 hybrids between Accession 160 and Bison was 4.1 grams.

Average weights of fruits of 14 homozygous immune plants in an F_2 progeny, identified by progeny tests, varied from 2.5 to 9.5 grams with an average of 4.7 grams. Fruits of 25 heterozygous plants in the same progeny varied from 2.5 to 8.5 grams with an average of 5.4 grams. Among 24 plants in another F_2 progeny, 1 had fruits averaging 17.5 grams in weight. The tendency of fruit size to vary but little more in F_2 than in F_1 progenies was quite obvious in observations of field-grown plants in different experiments; it would be expected because of the relatively large number of genetic factors affecting this character.

The back-cross method yielded plants with progressively larger fruits with comparatively small numbers of individuals in the progenies. Selection among 374 immune plants from the cross ((Bonny

Best x Accession 160) x Bonny Best) yielded 5 with fruits averaging 28.5 to 33.5 grams (Table 20). Since selection was based on other characters in addition to fruit weight, it is probable that some immune plants with larger fruits were not selected. Five selected hybrids among 116 immune selections from second back-crosses to Bonny Best had fruits averaging 42.0 to 70.0 grams (Table 20).

Table 20.—Average weights and numbers of locules in samples of tomato fruits of commercial varieties, Accession 160, and their hybrids. Field, Columbia, Missouri. 1937.

Variety or Cross	Number of Samples	Fruits per Sample	Weight in Grams	Number of Locules
Bonny Best	5	5	63.8	4
Bison	1	5	69.5	many
Break O'Day	5	5	62.5	5
Louisiana Pink	5	5	76.0	6
Oxheart	1	5	107.0	many
Ponderosa	5	5	159.0	many
Accession 160	9	1	1.2	2
Bonny Best x Accession 160, F_1	10	10	4.8	2
Bison x Accession 160, F_1	10	10	4.1	2
Bonny Best x Accession 160, F_2				
Heterozygous Immune	25	10	5.4	..
Homozygous Immune	14	10	4.7	..
Selected	1	10	17.5	..
(Bonny Best x Accession 160) x Bonny Best	1	5	33.5	4
	1	5	32.5	4
	1	5	30.0	4
	1	5	29.0	3
	1	5	28.5	3
(Bonny Best x Accession 160) x BB x BB	1	10	42.0	3
	1	5	70.0	3
	1	5	65.0	4
	1	5	52.5	many
	1	5	45.0	3
(BB x 160) x BB x Bison	1	10	51.0	4
	1	10	37.5	3
	1	5	55.0	3
	1	5	45.0	4
	1	5	60.0	5
(BB x 160) x Ox x Bison	1	10	51.0	5
	1	10	55.0	many
	1	10	39.0	many
	1	5	93.0	many
	1	5	66.0	many
(Earl x 160) x BD x Bison	1	5	65.0	many
	1	5	52.5	many
	1	5	40.0	6
	1	5	65.0	many
	1	5	40.0	7

Occasional fruits on plants in other second back-cross progenies weighed from 100 to 200 grams; however, most of the fruits were considerably smaller. Samples of 5 and 10 fruits from single plants, selected for other characters, particularly fruit quality, yielded averages as high as 93 grams (Table 20).

Among later generations tested in 1938, progenies from back-crosses to commercial varieties were more uniform in all characters

than progenies from self-pollinated hybrids. Several plants in all progenies, particularly in the back-cross progenies, had fruits similar in many respects to fruits of commercial varieties grown in the same field (Figure 9). Several plants in the progenies from self-pollinated flowers of second back-cross selections bore fruits with excellent quality and weighing approximately 60 grams; a few bore fruits weighing as much as 100 grams (Figure 9, A). Several plants in the third back-cross progenies bore fruits weighing 100 grams; a few bore fruits considerably larger (Figure 9; B, C).

Several plants from ((Earliana x Accession 160) x Break O'Day-selfed x Ponderosa)-selfed had extremely large fruits weighing as much as 260 grams.

First, second and third self-progenies from various back-cross selections yielded a large number of plants with good fruit characters, comparable with commercial varieties. Several of the second and third self-progenies were homozygous for immunity. Successive generations from self-pollinated flowers of selected hybrids are expected to yield a tomato homozygous for morphological characters as well as immunity.

11. SUMMARY

Seedling and field tests of the resistance of several wilt-resistant, commercial varieties of tomatoes to *Fusarium lycopersici Sacc.* (*F. bulbigenum* var. *lycopersici* Woll. u. Reink.) indicated that the resistance of these varieties is not effective under conditions very favorable for the development of the disease.

All accessions of *Lycopersicon esculentum* Mill., either cultivated or wild, were susceptible in some degree.

All species in other genera of the Solanaceae tested were immune to *Fusarium lycopersici.*

Tests of *Lycopersicon pimpinellifolium* Mill. showed that some accessions were very susceptible, some were partially resistant, and 1, Accession 160, possessed a degree of resistance which approached immunity and was so designated to distinguish it from the type of resistance occurring in commercial, resistant varieties.

The immunity of Accession 160 was maintained in greenhouse and field tests from 1935 to 1939 under conditions that resulted in almost universal infection of resistant commercial tomato varieties.

Attempts to induce wilt in Accession 160 by injecting suspensions of the fungus into stems were not successful.

Infection trials with 39 virulent isolates of *Fusarium lycopersici* from various regions and varieties failed to cause recognizable symptoms of the disease in Accession 160.

F_1 hybrids between Accession 160 and susceptible varieties were immune.

Tests of 1784 individuals from flowers of F_1 hybrids pollinated with pollen of commercial varieties yielded 854 suscepts and 930 immune plants. Second back-crosses from pollinations made in the same direction tested under conditions very favorable for wilt segregated 458 suscepts and 461 immune plants, demonstrating that immunity depends on a single dominant genetic factor.

In other experiments second, third, and fourth back-cross progenies and first, second and third self-progenies from successive back-crosses yielded proportions of immune and susceptible plants which demonstrated that the potency of the immunity factor is not decreased in association with large numbers of genetic factors from commercial varieties.

F_2 progenies and first back-crosses to commercial varieties using pollen of hybrids segregated proportions of suscepts smaller than would be expected on the basis of single factor inheritance. Data on F_3 progenies from the original cross; second back-crosses from flowers pollinated with pollen of hybrids; and first, second, and third self-progenies from successive back-cross selections demonstrated that the gene for immunity is linked with a factor influencing the effectiveness of the microgamete.

Selection in successive generations among plants grown in steamed, infested soil in the greenhouse and inoculated at transplanting in the field, yielded plants homozygous for the factor for immunity and bearing medium-large fruits of good quality. The plants were not homozygous for fruit and plant characters.

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13. APPENDIX

A. List of Accessions[1]

Accession	Species or Variety	Received from	Date
1	Marglobe	Burgess Seed and Plant Co. Galesburg, Michigan	1934
2	Pritchard	Burgess Seed and Plant Co. Galesburg, Michigan	1934
3	Break O'Day	Burgess Seed and Plant Co. Galesburg, Michigan	1934
4	Norton	Burgess Seed and Plant Co. Galesburg, Michigan	1934
5	Earliana	Burgess Seed and Plant Co. Galesburg, Michigan	1934
6	Bonny Best	Burgess Seed and Plant Co. Galesburg, Michigan	1934
7	Globe	Peter Henderson & Co. New York, New York	1934
8	Stone	Peter Henderson & Co. New York, New York	1934
9	Louisiana Pink	Reuter Seed Co. New Orleans, Louisiana	1934
10	*Lycopersicon pimpinellifolium*	R. v. Sengbusch Muncheberg, Germany	1934
11	Genetic stock d r y c a l	E. W. Lindstrom 1655-2 Ames, Iowa	1934
12	Genetic stock c l u d_2	E. W. Lindstrom 1656-5 Ames, Iowa	1934
13	Genetic stock d p o s r y	E. W. Lindstrom 1660-5 Ames, Iowa	1934
14	Genetic stock d_2	E. W. Lindstrom 1662-4 Ames, Iowa	1934
15	Genetic stock r y d p o s	E. W. Lindstrom 1388-4 Ames, Iowa	1934
16	*Lycopersicon pimpinellifolium*	E. W. Lindstrom 1965-4 Ames, Iowa	1934
17	*Lycopersicon pimpinellifolium*	E. W. Lindstrom 1546-7 Ames, Iowa	1934
18	*Solanum nigrum* L.	G. F. Weber Gainesville, Florida	1934
19	*S. capsiatrum* (*S. Capsicastrum* Link?)	G. F. Weber Gainesville, Florida	1934
20	*S. ledorodosum* (*S. heterodoxum* Dun?)	G. F. Weber Gainesville, Florida	1934
21	*S. sisymbrifolium* Lam.	G. F. Weber Gainesville, Florida	1934
22	*Solanum nigrum* L.	G. F. Weber Gainesville, Florida	1934

[1]Specific names were checked in Jackson, B. D. Index Kewensis, Oxford, Clarendon Press, M DCCC XCV.

Accession	Species or Variety	Received from	Date
23	*Solanum munistrum*?	G. F. Weber Gainesville, Florida	1934
24	*Solanum aculeatissimum* Jacq.	G. F. Weber Gainesville, Florida	1934
25	*Lycopersicon pimpinellifolium*	G. F. Weber Gainesville, Florida	1934
26	*Solanum rostratum* Dun.	G. F. Weber Gainesville, Florida	1934
27	*Solanum heterodoxum* Dun.	G. F. Weber Gainesville, Florida	1934
28	*Solanum sanitwongsei* Craib.	G. F. Weber Gainesville, Florida	1934
29	*Solanum verbascifolium* L.	G. F. Weber Gainesville, Florida	1934
30	*Solanum Dulcamara* L.	G. F. Weber Gainesville, Florida	1934
31	*Solanum bahamense* L.	G. F. Weber Gainesville, Florida	1934
32	*Nicandra physaloides* Gaertn.	G. F. Weber Gainesville, Florida	1934
33	*Lycopersicon esculentum*	G. F. Weber Gainesville, Florida	1934
34	*Lycium carolineanum* Walt.	G. F. Weber Gainesville, Florida	1934
35	*Solanum pseudocapsicum* L.	Dep't of Horticulture Univ. of Missouri	1934
37	*Solanum Fendleri* Huerck. e. Muell. Arg.	Donald Reddick Ithaca, New York	1934
38	*Solanum Commersonii* Dun.	Donald Reddick Ithaca, New York	1934
39	*Solanum Commersonii* Dun.	Donald Reddick Ithaca, New York	1934
40	*Solanum Jamesii* Torr.	Donald Reddick Ithaca, New York	1934
41	*Solanum Maglia* Schlecht.	Donald Reddick Ithaca, New York	1934
42	*Solanum polyadenium* Greenm.	Donald Reddick Ithaca, New York	1934
43	*Solanum chacoense* Bitter	Donald Reddick Ithaca, New York	1934
46	*Solanum demissum* Lindl.	Donald Reddick Ithaca, New York	1934
47	*Solanum antipoviczii* Buk.	Donald Reddick Ithaca, New York	1934
48	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
49	*Solanum demissum* Lindl.	Donald Reddick Ithaca, New York	1934

Accession	Species or Variety	Received from	Date
50	*Solanum ajuscoense* Buk.	Donald Reddick Ithaca, New York	1934
51	*Solanum demissum* Lindl.	Donald Reddick Ithaca, New York	1934
52	*Solanum demissum* Lindl.	Donald Reddick Ithaca, New York	1934
53	*Solanum demissum* Lindl.	Donald Reddick Ithaca, New York	1934
54	*Solanum demissum* Lindl.	Donald Reddick Ithaca, New York	1934
55	*Solanum demissum* Lindl.	Donald Reddick Ithaca, New York	1934
59	Solanum hybrid	Donald Reddick Ithaca, New York	1934
64	*Solanum sambucinum* Rydb.	Donald Reddick Ithaca, New York	1934
65	*Solanum aethiopicum* Jacq.	Donald Reddick Ithaca, New York	1934
66	*Solanum Khasianum* C. B. Clark	Donald Reddick Ithaca, New York	1934
67	*Solanum Khasianum* C. B. Clark	Donald Reddick Ithaca, New York	1934
68	*Solanum nigrum* L.	Donald Reddick Ithaca, New York	1934
69	*Solanum goniocalyx* Juzep. and Buk.	Donald Reddick Ithaca, New York	1934
70	*Solanum andigena* Juzep. and Buk.	Donald Reddick Ithaca, New York	1934
71	*Solanum andigena* Juzep. and Buk.	Donald Reddick Ithaca, New York	1934
72	*Solanum andigena* Juzep. and Buk.	Donald Reddick Ithaca, New York	1934
73	*Solanum andigena* Juzep. and Buk.	Donald Reddick Ithaca, New York	1934
74	*Solandigena andigena* Juzep. and Buk.	Donald Reddick Ithaca, New York	1934
75	*Solanum demissum* Lindl.	Donald Reddick Ithaca, New York	1934
76	*Solanum antipoviczii* Buk.	Donald Reddick Ithaca, New York	1934
77	*Solanum acaule* Bitter	Donald Reddick Ithaca, New York	1934
78	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
79	*Solanum nigrum* L.	Donald Reddick Ithaca, New York	1934
80	*Solanum sp.*	Donald Reddick Ithaca, New York	1934

Accession	Species or Variety	Received from	Date
81	*Solanum adjuscoense* Buk.	Donald Reddick Ithaca, New York	1934
82	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
85	*Solanum Otites* Dun.	Donald Reddick Ithaca, New York	1934
88	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
90	*Solanum verbascifolium* L.	Donald Reddick Ithaca, New York	1934
91	*Solanum Kantonnetii* Carr.	Donald Reddick Ithaca, New York	1934
92	*Solanum Warsyewiczii* Hort.	Donald Reddick Ithaca, New York	1934
93	*Solanum mammosum* L.	Donald Reddick Ithaca, New York	1934
94	*Solanum chloropetalon* Schlecht.	Donald Reddick Ithaca, New York	1934
101	*Solanum ciliolatum* Mart. e. Gal.	Donald Reddick Ithaca, New York	1934
102	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
104	*Solanum melongena* L.	Donald Reddick Ithaca, New York	1934
105	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
106	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
107	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
109	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
113	*Solanum tenancingo*?	Donald Reddick Ithaca, New York	1934
115	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
118	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
120	*Solanum pseudocapsicum* L.	Donald Reddick Ithaca, New York	1934
121	*Solanum Melongena* L.	Donald Reddick Ithaca, New York	1934
122	*Solanum sp.*	Donald Reddick Ithaca, New York	1934
123	*Solanum Camargo*?	Donald Reddick Ithaca, New York	1934
126	*Solanum cornutum* Lam.	Donald Reddick Ithaca, New York	1934

Accession	Species or Variety	Received from	Date
131	*Solanum Melongena* L.	Ferry-Morse Seed Co. Detroit, Michigan	1935
132	*Lycopersicon esculentum* (wild)	H. L. Blood Logan, Utah	1934
133	*Lycopersicon esculentum* (wild)	H. L. Blood Logan, Utah	1934
134	Stone	H. L. Blood Logan, Utah	1934
135	Illinois Pride	W. A. Huelsen Urbana, Illinois	1935
136	*Lycopersicon esculentum* (Turkey)	U. S. Dep't Agr. F. P. I. 109,112	1935
137	*Lycopersicon esculentum* (Turkey)	U. S. Dep't Agr. F. P. I. 109,113	1935
138	*Lycopersicon esculentum* (Turkey)	U. S. Dep't Agr. F. P. I. 109,512	1935
139	*Lycopersicon esculentum* (Turkey)	U. S. Dep't Agr. F. P. I. 109,513	1935
140	*Lycopersicon esculentum* (Turkey)	U. S. Dep't Agr. F. P. I. 109,514	1935
141	*Lycopersicon esculentum* (Turkey)	U. S. Dep't Agr. F. P. I. 109,315	1935
142	*Lycopersicon esculentum* (Turkey)	U. S. Dep't Agr. F. P. I. 109,316	1935
145	*Lycopersicon pimpinellifolium* (Peru)	E. W. Lindstrom Ames, Iowa	1934
146	*Lycopersicon pimpinellifolium* (Peru)	E. W. Lindstrom Ames, Iowa	1934
147	*Lycopersicon esculentum* (Italy)	E. W. Lindstrom Ames, Iowa	1934
148	*Lycopersicon esculentum* (Guatemala)	E. W. Lindstrom Ames, Iowa	1934
149	*Lycopersicon esculentum* (Oahu, T. H.)	E. W. Lindstrom Ames, Iowa	1934
150	*Lycopersicon esculentum* (Philippines)	E. W. Lindstrom Ames, Iowa	1934
152	*Physalis peruviana* L. (Mexico)	U. S. Dep't Agr. F. P. I. 103,722	1935
153	*Lycopersicon esculentum* (Australia)	U. S. Dep't Agr. F. P. I. 105,225	1934
155	*Solanum heterodoxum* Dun. (Germany)	U. S. Dep't Agr. F. P. I. 108,247	1935
156	Pear tomato (Germany)	U. S. Dep't Agr. F. P. I. 108,246	1935
157	Cherry tomato (Germany)	U. S. Dep't Agr. F. P. I. 108,245	1935
158	Yellow Tomato (Germany)	U. S. Dep't Agr. F. P. I. 108,244	1935

Accession	Species or Variety	Received from	Date
159	*Lycopersicon pimpinellifolium*	W. S. Porte 2515. U. S. Dep't Agr. P. Q. C. A. 04576	1935
160	*Lycopersicon pimpinellifolium* (Peru)	W. S. Porte 2116. U. S. Dep't Agr. P. Q. C. A. 0997	1935
161	*Solanum demissum* Lindl.	S. Bukasov Russia	1935
162	*Solanum demissum* Lindl.	S. Bukasov Russia	1935
163	*Solanum demissum* Lindl.	S. Bukasov Russia	1935
169	*Solanum neo-Antipoviczii* Buk.	S. Bukasov Russia	1935
171	*Lycopersicon esculentum*	S. Bukasov 732 Russia	1935
172	*Lycopersicon esculentum*	S. Bukasov 341 Russia	1935
173	Pear tomato	S. Bukasov 363 Russia	1935
174	*Lycopersicon pimpinellifolium*	S. Bukasov 1565 Russia	1935
175	*Lycopersicon esculentum*	Sec. de Agr. y Fomento Mexico City, Mexico	1935
176	*Lycopersicon esculentum*	Sec. de Agr. y Fomento Mexico City, Mexico	1935
177	*Lycopersicon esculentum*	Sec. de Agr. y Fomento Mexico City, Mexico	1935
178	*Lycopersicon esculentum*	Sec. de Agr. y Fomento Mexico City, Mexico	1935
179	*Lycopersicon esculentum*	Sec. de Agr. y Fomento Mexico City, Mexico	1935
195	*Lycopersicon esculentum* (native)	S. Wakabayashi 404 Hawaii	1935
202	Myco 1 tomato	T. Fahmy Giza, Egypt	1935
278	Cherry tomato	Royal Gardens 101 Kew, England	1936
279	*Lycopersicon pimpinellifolium* (red)	Royal Gardens 102 Kew, England	1936
281	*Lycopersicon pimpinellifolium* (yellow)	Royal Gardens 104 Kew, England	1936
317	Pear tomato (native)	F. P. Mehrlich Honolulu, Hawaii	1935
364	White Beauty	Burgess Seed and Plant Co. Galesburg, Michigan	1935
365	John Baer	Burgess Seed and Plant Co. Galesburg, Michigan	1935
366	Bison	Burgess Seed and Plant Co. Galesburg, Michigan	1935

Accession	Species or Variety	Received from	Date
367	Colossal	Burgess Seed and Plant Co. Galesburg, Michigan	1935
368	Earliest and Best	Burgess Seed and Plant Co. Galesburg, Michigan	1935
379	Urbana Forcing	W. A. Huelsen Urbana, Illinois	1936
384	Greater Baltimore	W. A. Huelsen Urbana, Illinois	1936
397	Selection 216-2-3 tomato	A. F. Jeager Fargo, North Dakota	1937
398	Fargo Yellow Pear	A. F. Jeager Fargo, North Dakota	1937
399	Bison	A. F. Jeager Fargo, North Dakota	1937
400	Pinkheart	A. F. Jeager Fargo, North Dakota	1937
401	Ponderosa	Ferry-Morse Seed Co. Detroit, Michigan	1937
423	Selection 209-2-10 tomato	A. F. Jeager Fargo, North Dakota	1937
425	Yellow Ponderosa	Wilhite Seed Store Columbia, Missouri	1937
468	Fusarium-wilt-resistant John Baer	M. C. Strong Michigan State College	1937
476	Bonny Best	Vaughan's Seed Store Chicago, Illinois	1937
477	Break O'Day	Vaughan's Seed Store Chicago, Illinois	1937
486	Ponderosa	Mueller, Florist Columbia, Missouri	1937
487	Bonny Best	Peter Henderson and Co. New York, New York	1935
488	Oxheart	Ferry-Morse Seed Co. Detroit, Michigan	1937
489	Yellow Pear	Dep't of Horticulture Univ. of Missouri	1935
490	*Lycopersicon pimpinellifolium*	Sup't Institute de Altos Estudios Agricolas del Peru. La Molina, Peru	1936
491	*Lycopersicon pimpinellifolium*	W. B. Dreer Philadelphia, Pa.	1939
492	*Capsicum annuum*	Ferry-Morse Seed Co. Detroit, Michigan	1935

B. List of Isolates

Isolate F 1 Culture received August, 1935, from Dr. R. J. Noble, Sydney, New South Wales. Isolated from a tomato plant.

Isolate F 2 Culture received September, 1935, from Dr. L. Petri, Rome, Italy. Isolated from a tomato plant grown in Puglia, Italy.

Isolate F 3 Isolated June, 1935, from *Lycopersicon pimpinellifolium* Accession 160 growing in a wheat culture of Isolate F 6, Columbia, Missouri.

Isolate F 4 Isolated July, 1935, from Bonny Best grown in autoclaved soil infested with a pure culture of Isolate F 11.

Isolate F 5a Isolated May, 1935, from Marglobe grown in autoclaved soil, Columbia, Missouri.

Isolate F 5b Isolated January, 1937, from a plate culture of Isolate F 5a on acidified potato-dextrose agar.

Isolate F 6 Isolated October, 1933, from a Marglobe tomato, Columbia, Missouri. Originally listed as C. M. Tucker's #160.

Isolate F 7 Isolated June, 1934, from a tomato plant received from Mr. I. F. Kennedy, St. Louis, Missouri.

Isolate F 8 Isolated May, 1935, from a Break O'Day tomato plant received from Mr. H. W. Guengerich, Kansas City, Missouri.

Isolate F 9 Identical with Isolate F 8.

Isolate F 10 Isolated May, 1935, from a Pritchard tomato plant grown in autoclaved soil, Columbia, 1935.

Isolate F 11 Isolated August, 1926, from a tomato stem, Columbia, Missouri. A monosporic isolate originally listed as C. M. Tucker's #111.

Isolate F 12 Culture received, 1934, from C. L. Lefebvre, Kansas Agricultural Experiment Station, Manhattan, Kansas. Originally listed as C. M. Tucker's #150.

Isolate F 13 Culture received, 1934, from C. L. LeFebvre, Kansas Agricultural Experiment Station, Manhattan, Kansas. Originally listed as C. M. Tucker's #151.

Isolate F 14 Isolated April, 1935, from an Illinois Pride tomato plant grown in autoclaved soil, Columbia, Missouri.

Isolate F 15 Culture received February, 1936, from Mr. N. S. Shirlow, Hawkesbury Agricultural College, Richmond, New South Wales.

Isolate F 16 Identical with F 15.

Isolate F 17 Culture received February, 1936, from Dr. C. D. Sherbakoff, through Dr. J. R. Underwood, Knoxville, Tennessee. Originally listed as Dr. Sherbakoff's #899.5, from Riverside, California.

Isolate F 18 Culture received, February, 1936, from Dr. C. D. Sherbakoff, through Dr. J. R. Underwood, Knoxville, Tennessee. Originally listed as Dr. Sherbakoff's #1210.5, from Georgia.

Isolate F 19 Culture received February, 1936, from Dr. C. D. Sherbakoff, through Dr. J. R. Underwood, Knoxville, Tennessee. Originally listed as Dr. Sherbakoff's #1273.1 from Kentucky.

Isolate F 20 Culture received February, 1936, from Dr. C. D. Sherbakoff, through Dr. J. R. Underwood, Knoxville, Tennessee. Originally listed as Dr. Sherbakoff's #1279.

Isolate F 21 Culture received February, 1936, from Dr. C. D. Sherbakoff, through Dr. J. R. Underwood, Knoxville, Tennessee. Originally listed as Dr. Sherbakoff's #1303.16, from Athens, Georgia.

Isolate F 22 Culture received February, 1936, from Dr. C. D. Sherbakoff, through Dr. J. R. Underwood, Knoxville, Tennessee. Originally listed as Dr. Sherbakoff's #1322.43, from Michigan.

Isolate F 23 Culture received February, 1936, from Dr. C. D. Sherbakoff, through Dr. J. R. Underwood, Knoxville, Tennessee. Originally listed as Dr. Sherbakoff's #1385, from Knoxville, Tennessee.

Isolate F 24 Culture received February, 1936, from Dr. C. D. Sherbakoff, through Dr. J. R. Underwood, Knoxville, Tennessee. Originally listed as Dr. Sherbakoff's #1316.

Isolate F 25 Isolated, February, 1936, from a Break O'Day tomato plant grown in the greenhouse of the Department of Horticulture, University of Missouri, Columbia, Missouri.

Isolate F 26 Isolated February, 1936, from a Break O'Day tomato plant grown in the greenhouse of the Department of Horticulture, University of Missouri, Columbia, Missouri.

Isolate F 27 Isolated February, 1936, from a Break O'Day tomato plant grown in the greenhouse of the Department of Horticulture, University of Missouri, Columbia, Missouri.

Isolate F 28 Isolated February, 1936, from a Break O'Day tomato plant grown in the greenhouse of the Department of Horticulture, University of Missouri, Columbia, Missouri.

Isolate F 29 Isolated from tomato stems received March, 1936, from the mycologist at the Tropical Research Station, Nelspruit, South Africa, through Dr. J. D. J. Hofmeyer.

Isolate F 30 Isolated from tomato stems received March, 1936, from the mycologist at the Tropical Research Station, Nelspruit, South Africa, through Dr. J. D. J. Hofmeyer.

Isolate F 31 Isolated from tomato stems received March, 1936, from the mycologist at the Tropical Research Station, Nelspruit, South Africa, through Dr. J. D. J. Hofmeyer.

Isolate F 32 Isolated from tomato stems received March, 1936, from the mycologist at the Tropical Research Station, Nelspruit, South Africa, through Dr. J. D. J. Hofmeyer.

Isolate F 33 Isolated from tomato stems received March, 1936, from the mycologist at the Tropical Research Station, Nelspruit, South Africa, through Dr. J. D. J. Hofmeyer.

Isolate F 34 Isolated February, 1936, from tomato culture 5-727-1, an F_1 hybrid between Bonny Best and *Lycopersicon pimpinellifolium* Accession 160. Isolated from stem.

Isolate F 35 Isolated February, 1936, from tomato culture 5-727-1, an F_1 hybrid between Bonny Best and *Lycopersicon pimpinellifolium* Accession 160. Isolated from root.

Isolate F 36 Isolated February, 1936, from tomato culture 5-727-2, an F hybrid between Bonny Best and *Lycopersicon pimpinellifolium* Accession 160. Isolated from stem.

Isolate F 37 Isolated February, 1936, from tomato culture 5-727-2, an F_1 hybrid between Bonny Best and *Lycopersicon pimpinellifolium* Accession 160. Isolated from root.

Isolate F 40 Isolated June, 1936, from tomato field culture 6-700-16, a back-cross of Earliana x Accession 160 to Accession 160.

Isolate F 41 Culture received 1936, from Dr. S. P. Doolittle, Senior Pathologist, Horticultural Field Station, Beltsville, Maryland. Originally listed as Dr. Doolittle's culture #2, as the strain used by Pritchard and Porte in most of their early work.

Isolate F 42 Culture received 1936, from Dr. S. P. Doolittle, Senior Pathologist, Horticultural Field Station, Beltsville, Maryland. Originally listed as Dr. Doolittle's #93, from a field on Sneed's Island, near Bradenton, Florida.

Isolate F 43	Culture received 1936, from Dr. S. P. Doolittle, Senior Pathologist, Horticultural Field Station, Beltsville, Maryland. Originally listed as Dr. Doolittle's #94, "Collected near Terra Ceia, which is also near Bradenton, Florida."
Isolate F 44	Isolated October, 1936, from tomato culture 6-700-16, a backcross of Earliana x Accession 160 to Accession 160, grown in the tomato wilt test plot, Columbia, Missouri.
Isolate F 45	Isolated October, 1936, from tomato culture 6-702-12, a backcross of Earliana x Accession 160 to Accession 160, grown in the tomato wilt test plot, Columbia, Missouri.
Isolate F 46	Isolated June, 1938, from a Red Rock tomato plant received from Dr. P. A. Young, Tomato Disease Laboratory, Jacksonville. Texas.
Isolate F 47	Isolated June, 1938, from a Riverside tomato plant received from Dr. P. A. Young, Tomato Disease Laboratory, Jacksonville, Texas.
Isolate F 48	Isolated June, 1938, from a Louisiana Red tomato plant received from Dr. P. A. Young, Tomato Disease Laboratory, Jacksonville, Texas.
Isolate F 49	Isolated June, 1938, from an Illinois Baltimore tomato plant received from Dr. P. A. Young, Tomato Disease Laboratory, Jacksonville, Texas.
Isolate F 50	Isolated June, 1938, from a Red Rock tomato plant received from Dr. P. A. Young, Tomato Disease Laboratory, Jacksonville, Texas.
Isolate F 51	Isolated June, 1938, from a Gulf State Market tomato plant received from Dr. P. A. Young, Tomato Disease Laboratory, Jacksonville, Texas.